The Role of Seed Dispersal, Seed Predation and Drought in the Restoration of Ngel Nyaki Forest, Nigeria

A thesis submitted in partial fulfilment of the requirements for the degree of

MASTER OF SCIENCE in ECOLOGY

By
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Abstract

The restoration of degraded landscapes has become one of our most valuable tools for conservation, however there are many factors which can restrict natural regeneration and impede active restoration attempts. The purpose of this study was to investigate three key processes which commonly limit the establishment of forest tree species into abandoned pasture in tropical forests: i) dispersal limitation, ii) seed predation, and iii) competition from the grass sward.

Seed dispersal

I identified 59 species of birds that were using the grassland habitat. Through 216 hours of focal tree observations I established that isolated trees in the grassland that had larger canopies, and those that were providing a food source (i.e. flowers or fruit) had significantly higher bird visitation rates and average stay lengths. I found evidence of the "perch effect" as patches of remnant trees encouraged more birds into areas of grassland, and the density of seedlings under tree canopies was significantly positively correlated with bird visitations. 95% of the seedlings found beneath tree canopies in grassland were of a different species to that of the tree canopy above them, demonstrating the dispersal of seeds from elsewhere into these microhabitats. 98% of these seedlings are grassland or forest edge species showing forest core species are still dispersal or microsite limited despite the effect of these trees.

Seed predation

Removal rates of seeds from experimentally laid out seed piles varied among seed species, the habitat the pile was in, and the predator guild able to access the piles. Preliminary results indicate that these trends are driven by the ecology of the seed predator. Removal of seeds by vertebrates was highest in the core forest, while ant predation was constant across all habitats. Vertebrates removed the larger seeds (*Entandrophragma angolense* and *Sterculia tragacantha*) while ants preferred the smaller *Celtis gomphophylla* and *Croton macrostachyus*. Overall predation rates in grassland were lower than those

in the forest, and the presence of remnant trees did not influence predation rates, a positive sign for regeneration and the survival of seeds dispersed into these areas.

Competition from the grass sward

While the grass sward provides shade for seedlings of forest tree species it is also a harsh environment for them, as the grass competes with seedlings for water. Removing the grass and covering planted seedlings with artificial shading structures significantly increased both the survival and growth of these seedlings.

Recommendations

From this study I was able to make recommendations for a low input restoration program at Ngel Nyaki. Planting seedlings in small 'islands' takes advantage of the natural increase in dispersal of seeds under isolated trees, while low seed predation rates increase the chance of survival of these seeds to germination. Planting these seedlings under shade will lead to increases both their growth rates and their survival. Once the secondary forest develops, under-planting seedlings of core forest trees will introduce them to the system, as the natural establishment of these seeds appears to be limited in the current environment. This study has also served to remind us how little we know about this particular forest-grassland system, and has led to the development of ideas for further investigations into several more aspects of regeneration.

Chapter 1: Introduction

Restoration Ecology, Ngel Nyaki Forest, and Thesis Outline

1.1 Restoration Ecology

Deforestation

Throughout history humans have utilised natural lands to gain resources but this use is becoming increasingly unsustainable (Desvaux, 2007). In many developing countries throughout the world, such as in Asia and Africa, the human population is continuing to increase rapidly, which in turn places increasing pressure on forests and other natural areas for food, fuel and farmland (Parrotta et al., 1997). Large tracts of land are being cleared or burnt to provide these resources (Aide et al., 2000; Fearnside, 2005) and the rate of this deforestation continues to be a major concern. Globally 13 million hectares of forest was been converted to other uses between 2005 and 2010 (Food and Agriculture Organisation of the United Nations, 2010), with tropical forests one of the most badly affected ecosystems (Parrotta et al., 1997), showing an "astonishingly rapid decline" (Lamb et al., 2005) in the last century.

Deforestation both reduces total forest area and increases fragmentation, which have flow on effects to the entire forest community and to human populations in the area (Parrotta et al., 1997). Habitat loss is one of the major causes of species decline and extinction, having been identified as a source of risk to over 70% of threatened species (Owens & Bennett, 2000). Tropical forests contain some of the highest biodiversity in the world (Aide et al., 2000; Fearnside, 2005) so that their loss is particularly concerning. Forests are also major players in global water and carbon cycles (Aide et al., 2000; Fearnside, 2005) as well as affecting climate (Achard et al., 2002), so that their reduction has wide ranging effects. Deforestation also negatively impacts human populations inhabiting the area through a reduction in basic ecosystem services such as increasing water quality. An estimated 300 million people in developing countries are currently relying on degraded forests for their livelihoods (International Tropical Timber Organization, 2002).

Regeneration

Much land that has been deforested in the past has now been abandoned due to decreased productivity, or social and economic factors (Parrotta et al., 1997; Aide et al., 2000). These abandoned lands provide opportunities for restoration for both conservation purposes and the improvement of ecosystem services (Parrotta et al., 1997; Lamb et al., 2005). Restoration cannot replace the importance of preventing further destruction of primary forests as the restored systems are seldom the same as the original (Zedler, 2000). However restoration is a promising and effective tool for reversing the damage that has already been done (Hobbs & Norton, 1996; Reay & Norton, 1999; Hobbs & Harris, 2001; Cortina et al., 2006) and can increase biodiversity and restore environmental services (Benayas et al., 2009). As a result, in recent years the science of restoration ecology has developed in the literature to become one of the fastest growing areas in conservation biology (Young, 2000; Choi, 2004).

Natural succession

Often secondary forest will develop on degraded agricultural land after abandonment if disturbance factors are removed (Dobson et al., 1997; Parrotta et al., 1997; Prach et al., 2001; Suding et al., 2004). The expectation that this is enough to promote regeneration is based in the historical theory of climax communities (Connell & Slatyer, 1977; Cortina et al., 2006), theoretically if a system was left to recover naturally then it should follow a linear path (the reverse of the degradation) back to the original system (Suding & Hobbs, 2009) because the climax community was best suited to the local climatic conditions (Clements, 1916). A major appeal of this solution is that natural succession should require very little input of money or labour (Bradshaw, 1983) and is therefore very appealing for the restoration of large areas (Aide et al., 2000) or in places where there is little financial support for conservation.

However while natural succession has been used extensively around the world there have been varying degrees of success. If system disturbance has been minimal or only occurred for short periods of time, then recovery through natural succession may be very fast (Uhl, 1987; Arnold et al., 1999).

However the ability to regenerate decreases incrementally in relation to the severity and length of degradation and the type of change that has occurred (Uhl, 1988; Nepstad et al., 1991; Aide & Cavelier, 1994). Consequently in other systems recovery has not been as successful as was hoped (Holl et al., 2000; Paquette et al., 2006; Standish et al., 2007; Gunaratne et al., 2010). Often vegetation will establish but the recovering area has a significantly different species composition to the original system, while in other areas any succession remains severely restricted even after extended periods of time (Bradshaw, 1983; Zimmerman et al., 1995; Aide et al., 2000). This lack of natural regeneration is turning into a major problem with one estimate being that 350 million hectares of tropical forest land has been degraded to the point that it will not spontaneously regenerate (International Tropical Timber Organization, 2002)).

Barriers to regeneration

When a forest is cleared the area is usually rapidly colonised by grassland species. This grassland state is then kept stable by internal feedbacks that provide resilience to the system and stop it from changing with small scale perturbations (Beisner et al., 2003; Murphy & Bowman, 2012). Positive internal feedbacks occur when the presence of the grass alters environmental conditions to those that enhance the growth of the grass and restrict the re-establishment of the forest species. For example grasses can promote regular fires which destroy young forest seedlings before they are able to grow large enough to become more fire resistant, thus maintaining the area as grassland (Knox & Clarke, 2012; Murphy & Bowman, 2012). If these feedbacks are strong enough to prevent any natural regeneration at all, and the grassland state becomes permanent instead of a transition state, the system is then said to have crossed thresholds into an alternative stable state, where a further change of state is unlikely without more, large, perturbations (Suding et al., 2004). This situation is more likely to occur when the degradation is particularly severe or when it occurs over a long period of time. Not all degraded systems have crossed thresholds and have entered alternative stable states. However such threshold models are very important in restoration ecology as the same processes and internal feedbacks also create barriers that slow regeneration in other degraded areas. These barriers can be either abiotic (relating to changes in the physical environment) or biotic (changes in interactions

caused by differing species compositions) and most commonly there are multiple factors and feedbacks that are preventing the regeneration of a single system.

Examples of factors limiting passive forest regeneration in old pastures

Abiotic factors are those that relate to the environment of the system such as soil conditions, water levels and microclimate. Deforestation often leads to high levels of erosion and soil leaching (Yates et al., 2000; Zhao et al., 2005). Moreover lack of plant biomass turnover can lead to lower nutrient levels in grazed grassland which can restrict seedling growth (Aide & Cavelier, 1994; Zhao et al., 2005). Reduced canopy cover in grassland can have a direct effect on seedlings through an increase in solar radiation (Uhl, 1987), while a lack of shading also increases air and soil temperatures which in turn can affect soil moisture levels (Holl, 1999). These factors have been shown to cause water stress limiting seedling survival and growth in pasture (Nepstad et al., 1991).

Other abiotic changes are caused by biotic factors. Grasses are often fire promoting, especially compared to mature forest, which can alter the fire regime in these cleared areas (Hoffmann et al., 2012; Knox & Clarke, 2012). The use of heavy machinery in farming practices, or the trampling of cattle, causes soil compaction. This produces a physical barrier that prevents the roots of seedlings getting into the soil to establish and also changes soil hydrology (Yates et al., 2000) . Organic matter and other nutrients in the soil are often reduced by clearance and grazing (Olowolafe, 2008).

Biotic barriers occur when interactions between species change, having huge impacts on the structure and functioning of the system. Once the forest has been cleared the land is usually rapidly colonised by native or exotic grasses (Standish et al., 2007). The presence of a grass sward, or any other non-forest plants, has been found to be a major barrier to regeneration (Li et al., 2011; Thaxton et al., 2012), due to competition for nutrients, water, light, and space severely reducing the germination and survival of forest seedlings (Holl et al., 2000). Seed banks in cleared areas reduce over time which limits the ability of species to regenerate even after the degrading factors are removed (Bakker & Berendse, 1999). The habitat shift created by deforestation also changes plant-animal interactions

such as dispersal, seed predation, and herbivory (Gunaratne et al., 2010). Seeds of forest species may not be dispersed into grassland as forest-dwelling vertebrate dispersers do not spend so much time in the open grassland, while along forest edges regenerating seedlings are subject to herbivory and predation from both forest and grassland species.

Undertaking a restoration project

When undertaking a restoration project it is important to first establish the goals of the project and then choose management options that are within budget and that will make a useful contribution to the regeneration of the area. Failing to understand the processes restricting natural regeneration can impede even active restoration attempts. However if these processes are understood it may be possible to manipulate the system to overcome these barriers and reinstate natural regeneration. Managers need to consider a range of factors when starting a restoration project such as i) what factors are at play in that system, ii) what management practices are going to be used to overcome them, iii) what financial constraints are in place, and finally, what the final aim of the project is.

Techniques for restoration

The techniques chosen for a specific project will depend on priorities and objectives, cost/benefit analyses, and economic, social and environmental values (Lamb, 1994). If the system has strong internal feedbacks and is therefore very resistant to change, then major manipulation may be needed to prompt a change in state (Beisner et al., 2003). For example restoration planting is a widely used technique to overcome dispersal and germination limitation (Reay & Norton, 1999; Paquette et al., 2006; Omeja et al., 2011). It effectively 'speeds up' the recolonisation of forest species into grassland areas and the growth of these seedlings, thus promoting further biomass accumulation and biodiversity (Omeja et al., 2011). Controlled burning and/or grazing are used in some systems to remove exotic grasses that prevent the germination of seedlings (Hancock et al., 2009; Zimmermann et al., 2009). This technique is most often used in systems where fire is natural and human influence has prevented it from occurring. Other methods such as using plantations of commercially valuable trees to modify biological conditions (Parrotta et al., 1997; Lamb et al., 2005) and constructing

perches for birds (Holl, 1998a) have also been trialled. Limiting the usefulness of these methods is the fact that they are often very costly and are therefore not always practical for large areas or in developing countries.

Required information

While a solid conceptual framework is necessary to underpin successful restoration (Hobbs & Norton, 1996; Hobbs & Harris, 2001; Suding et al., 2004), even given this restoration efforts may still fail. Such a framework may provide an over simplification of the factors that are at work in any one specific system (Hilderbrand et al., 2005). Many systems will have multiple factors constraining them (Acácio et al., 2007) and manipulating too few, or the wrong factors for that particular system may result in no change at all (Byers et al., 2006). Moreover the long term objectives need to be realistic and tailored to the specific site (Ehrenfeld, 2000) and the desired outcomes of the project. Managers must have site specific, detailed, and accurate biological information of both the degraded and target systems (Ehrenfeld, 2000) in order to design a project that has the best chance of success.

1.2 West African Montane Forests

Almost all of the world's tropical forests are found in Africa, Asia and South America. Africa has the second highest loss in primary forests of these three areas (Food and Agriculture Organisation of the United Nations, 2010), and natural reforestation is also the most limited on this continent (Achard et al., 2002). It is also thought that in the future the impacts of climate change are going to affect Africa more than any other region (Fields, 2005). These factors mean the future and conservation of forests in Africa is of huge concern.

Afromontane forests are found on the mountain ranges of Africa, between 990 and 4000m altitude (White, 2008). These forests are floristically very similar but are separated from each other by large

expanses of lowland s with different floristic makeups. This pattern has led to many authors comparing the mountains to islands (although it must be realised that biogeographically the lowlands are very different to the sea) (Grimshaw, 2001). The term 'Afromontane Archipelago' as described by White (1978) is the most commonly used metaphor for this region (Fig. 1.1). The flora of the Afromontane ecosystems is very specialised – three quarters of the species are endemic or near endemic to Afromontane forests (White, 2008). Although a lot of literature has been published on the Afromontane region we still have a very limited understanding which needs to be extended in order to properly protect them from the current high levels of deforestation.

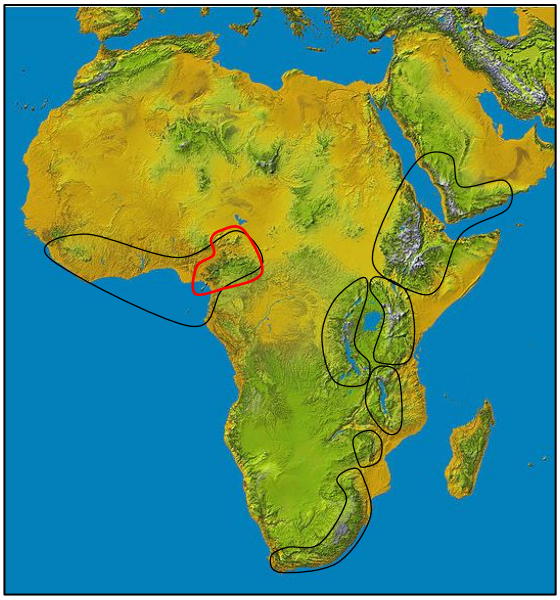


Figure 1.1 Map of the Afromontane zones that make up the Afromontane Archipelago. The Cameroonian Highlands are circled in red. Adapted from Wikimedia Commons (2011)

The Cameroonian Highlands is a chain of mountainous areas running from Mambilla Plateau in the North-East, along the Nigerian/Cameroon border, and terminating in the island of Bioko (Fig 1.2). The forests in this area are very vulnerable due to high deforestation rates in West Africa (Davis et al., 1994) coupled with the small proportion of total land area that montane and submontane forests cover (Sayer et al., 1992).

The Cameroonian Highland Region has high levels of endemism in many taxonomic groups including primates, birds, amphibians and vascular plants (Bergl et al., 2007), and thus should be a priority for conservation (Chapman et al., 2004) but this has not been reflected in the management and protection of these lands. Human populations are increasing in the area as the previously nomadic Fulani settle into villages (pers. comm.). Despite some forests being officially protected, this increasing demand for resources leads to more land being cleared for farming and grazing while poaching for bushmeat also continues (Chapman, 2008). What is left of these forests is highly degraded and fragmented (Chapman, 2008) and surrounded by farmland, which further exacerbates their losses.

1.3 Ngel Nyaki Forest Reserve

Ngel Nyaki forest (7°30'N, 11°30'E) is an Afromontane forest fragment, and the largest of those left on Mambilla Plateau, Nigeria (Fig. 1.2). The reserve covers an area between 1400 and 1600m in altitude. Soils are volcanic and overgrazing and reduced vegetation cover has led to leaching and erosion (Chapman & Chapman, 2001).

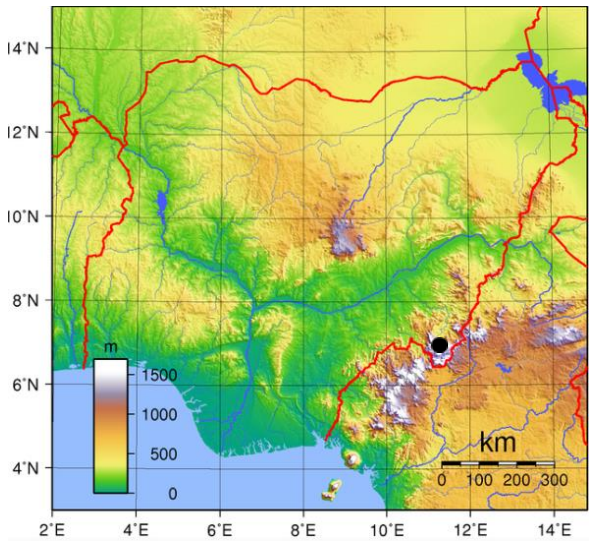


Figure 1.2. A relief map of Nigeria and western Cameroon showing the location of the Cameroonian Highlands Region. Location of Ngel Nyaki forest is marked by a black point. Adapted from Wikimedia Commons (2007).

There are two seasons, a dry season from November to March, followed by a rainy season from April to October during which almost all of the annual 1800mm of rain falls (Chapman & Chapman, 2001). Mean monthly maximum and minimum temperatures are 26 and 13°C for the wet season, and 23 and 16°C for the dry season (Matthesius et al., 2011). Ngel Nyaki is a broad-leaved, angiosperm forest surrounded by severely degraded tussock grasslands that are heavily grazed and burnt (Chapman, 2008). Relatively undisturbed primary forest makes up around 7km² of the 42km² Ngel Nyaki Forest Reserve in one contiguous escarpment forest, while highly disturbed smaller riparian fragments lie just outside the reserve boundary (Fig. 1.3).

Figure 1.3 Satellite photo of Ngel Nyaki forest with the boundary of the reserve superimposed. Adapted from Google Maps (2014)

Diversity

Ngel Nyaki is one of the most floristically diverse forests in Nigeria, containing several endemic plant species, and four of the tree species on the IUCN Red List: *Millettia conraui*, *Entandrophragma angolense*, *Lovoa trichilioides* and *Pouteria altissima* (Chapman & Chapman, 2001). The forest is also relatively abundant in birds and mammals despite the on-going poaching pressure. In 2001 Birdlife International designated Ngel Nyaki Forest Reserve as an Important Bird Area (BirdLife International, 2014) in recognition of its diversity of bird species, and eight primate species are found

here including populations of the Nigeria-Cameroonian Chimpanzee (*Pan troglodytes ellioti)* and the Putty-nosed Monkey *(Cercopithecus nictitans)* (Chapman & Chapman, 2001).

Degradation

The Ngel Nyaki forest was gazetted as a Forest Reserve in 1969 and it was maintained and patrolled throughout the 1970's (Chapman, 2008). From the 1980's onwards a lack of funding resulted in a decrease in the level of protection that the forest received. A survey of the forests in the area found that in the 30 years between 1972 and 2002 Ngel Nyaki forest had been further degraded due to low funding leading to poor patrolling and infrastructure (Chapman et al., 2004). The Nigerian Montane Forest Project (NMFP) was established in 2003 to both study and protect Ngel Nyaki Forest Reserve. Despite this increased protection, the forest still faces many threats. The human population on the Mambilla Plateau has been increasing since the 1970's (Chapman & Chapman, 2001) and this in turn has increased the demand for grazing land. Fulani herders have moved into the reserve and practice slash and burn agriculture which damages the understory and encroaches on the forest edge. Grazing cows in the forest and around the edges causes erosion and limits the survival of forest seedlings. Yearly burning of the grass both in the reserve and around the perimeter further halts natural succession into these areas (Fig. 1.4). Poaching for bushmeat still occurs, threatening populations of large mammals and birds though, with around 40 forest patrollers now under the employ of the NMPF and Department of Forestry, this has been greatly reduced.

Figure 1.4 Causes of degradation, (left) cows emerging from the forest edge, (right) farmers burning the grassland around the edge of the forest (photo: Idrisa Musa).

Restoration

One of the long term aims of the NMFP is to restore Ngel Nyaki forest out to the reserve boundary (Fig. 1.3). Five blocks of land around the forest edge have been progressively fenced off since 2006 to promote natural regeneration by protecting the areas from cattle grazing and burning (Fig. 1.5). All the experiments in this thesis were carried out in these fenced areas.

Figure 1.5 Satellite photo of part of Ngel Nyaki forest. The areas of abandoned pasture that have been fenced off have been outlined. Adapted from Google Maps (2014).

In these areas, different grasses are able to colonise along with many other herbaceous species and woody shrubs. This creates a sward often over 1m high with some colonising forest trees, such as *Albizia gummifera*, *Psorospermum corymbiferum*, and *Syzygium guineense*, (Campbell, 2010) scattered through (Fig 1.6). In these fenced-off areas the edges aren't well defined and tend to consist of a band of large herbs and shrubs. The degraded grassland surrounding the forest is dominated by the tough tussock *Sporobolus africanus*, and where the forest is not fenced the edge between the forest and the grassland is usually very abrupt as fires prevent the growth of shrubs and seedlings while not destroying the adult trees (Fig. 1.7).

Figure 1.6 Inside one of the fenced off and regenerating grassland areas around the forest edge. The grass is much longer than outside the fence and is indispersed with flowing herbs, non-woody shrubs, and woody tree saplings.

Figure 1.7 Looking across the forest from one of the eastern edges of the reserve. The burnt and grazed grassland gives way to mature forest very suddenly with very little edge habitat.

From the literature we know that it is common for farmland to not regenerate after abandonment (Cramer et al., 2008) for a variety of reasons as outlined above in "Examples of factors limiting passive forest regeneration from pasture". In order to promote natural regeneration in this forest we must have a solid knowledge of what factors are restricting succession in this particular system. Some restoration studies have already been carried out at Ngel Nyaki forest. Campbell (2010) has done a preliminary investigation of the effects offencing and the distance from the forest edge on seed bank, herbivory and seed predation rates. A study on the effects of distance on seed dispersal into grassland

has been completed (Barnes & Chapman, 2014) and a large seedling herbivory trial, across a range of habitats, is currently being set up. Despite this progress there are still gaps in our knowledge which, when filled, will give us a better understanding of this system.

1.4 Thesis Outline

The main focus of this study is on the reestablishment of forest tree species in the fenced-off grassland. In order for a tree from the forest to establish in the grassland, three steps must occur: i) seeds must be produced by an adult tree, ii) a seed must get from the forest into the grassland (dispersal), and iii) the seed must be able to germinate, survive and grow (Li et al., 2011). If any of these steps fails then regeneration will fail. I have run three different experiments looking at different processe across these last two steps to try and get an overview on which processes are most restricting regeneration in this particular system.

Specifically my research questions are:

1) What effects do remnant trees of different characteristics in grassland have on visitation rates of birds? How does this translate to seed rain levels under tree canopies?
2) Does the level of seed predation vary between microhabitat, and under trees in grassland?
3) Does the grass sward compete with or facilitate the growth of forest seedlings? What biotic and abiotic factors does the grass sward alter in order to have this effect?

In order for this project to have a practical use, we must be able to develop an applied management plan from our findings. The lack of funding and the huge scope of this restoration project means that low cost, large scale management that assists and directs natural regeneration is needed. A real focus of this study therefore is to use our increasing knowledge of this system to develop these low intensity management options.

Thesis Structure

Each question has been written up separately leading to Chapters 2, 3 and 4 being structured as three stand-alone papers. To try and minimise repetition between chapters the general information on the field site can be found within the introduction. However there is still a small amount of overlap between chapters.

Chapter 2: Seed Dispersal

Relationships between Characteristics of Isolated Trees, Bird Visitations and Seedling Survival

2.1 Introduction

2.1.1 Background to seed dispersal

Seed dispersal in regenerating forest ecosystems

Seed dispersal from the forest into degraded grassland is an essential process for the regeneration of these areas (Howe & Miriti, 2004), and this is especially so when seed banks are limited as they often are in Afromontane systems (Tekle & Bekele, 2000). The main dispersal mechanisms are vulnerable to disruption by forest fragmentation and loss (McConkey et al., 2012), and thus dispersal limitation is a major factor limiting plant recruitment in many degraded systems (Holl, 1999; Gunaratne et al., 2010). Lower numbers of seeds being dispersed away from the parent tree can be due to an overall reduction in frugivore numbers, either because smaller patches of forest support fewer animals, or because many larger-bodied animals cannot survive in small fragments (Cordeiro & Howe, 2003). Patterns of vertebrate-mediated seed dispersal can also be affected by fragmentation as the behaviour of the vectors can change in response to edges and degraded patches, while wind patterns can also be different around the edges of the forest compared with the forest core (Damschen et al., 2008).

Frugivorous birds as seed dispersers

A large proportion of tropical forest trees, between 50 and 75% depending on the system (Howe & Smallwood, 1982; Wunderle Jr, 1997), have fleshy fruits adapted for vertebrate dispersal. Birds are usually the major dispersers, followed by primates, bats, and canids (Duncan & Chapman, 1999; Cavallero et al., 2013). In order for vertebrate-dispersed seeds to travel from the forest to the grassland areas, the dispersing animals must travel between these habitats. Bird species differ in their tolerance to fragmented environments and their ability to utilise the grassland system (Calviño-Cancela, 2002; Prevedello & Vieira, 2010), and many forest-dwelling birds avoid going into open patches, preferring instead to stay within forested areas (Herrera & Garcia, 2010). For instance Da Silva et al. (1996) studied abandoned pastures adjacent to primary forest in Amazonia. They found

that out of a total of 47 frugivorous bird species found in the forest, only 18 were commonly observed in the regenerating grassland and only three used active agricultural land. Birds choose habitats based on many factors including food availability and protection from predators (Aben et al., 2012), and in general grassland is limited in both these aspects, especially for bird species from the core forest. As a result, bird-dispersed seed rain often declines rapidly with increasing distance from the forest edge (Holl, 1999; Cubiña & Aide, 2001; Ingle, 2003), leading to the dispersal limitation of these seeds in regenerating grassland (Duncan & Chapman, 1999). Only the bird species that move between forest and grassland habitats are useful vectors for seed dispersal for forest regeneration (Uhl et al., 1988), and so any factor that can encourage more frugivorous birds into the grassland may benefit regeneration through an increase in seed rain.

Seed dispersal is a major filtering process that determines what species will be present in the final system, and therefore has a major effect on community structure (Wang & Smith, 2002). For example, larger-seeded species from the forest core which rely on wide-gaped birds or primates for dispersal tend to be more dispersal limited, while small-seeded pioneer species more rapidly colonise abandoned pasture land (Howe & Miriti, 2004; Cramer et al., 2007). Such differences contribute to variation in species compositions between primary and secondary forests for extended periods of time (Uhl et al., 1988; Aide et al., 2000; Guariguata & Ostertag, 2001).

Effect of isolated trees on seed rain

Isolated trees, either remnants or early colonisers, provide focal points for passive regeneration in grassland (Uhl, 1987). They both attract frugivores which increases seed rain, and provide an enhanced microsite for seedling survival (Duncan & Chapman, 1999; Herrera & García, 2009; Cavallero et al., 2013). This effect has been termed the "Perch Effect" and has been found in cleared agricultural land across many different systems, both temperate and tropical (McDonnell & Stiles, 1983; Holl, 1998a; Duncan & Chapman, 1999; Herrera & García, 2009; Cavallero et al., 2013). Not all trees have the same effect on the seed rain because birds will visit some trees more than others. A huge range of tree characteristics have been found to contribute to bird choice including isolation,

height (McDonnell 1986), distance from the forest edge (Sheldon & Nadkarni, 2013), and the availability of fruit (Wunderle Jr, 1997).

2.1.2 Aims of this study

Dispersal limitation in grassland areas can be partially overcome by the presence of trees and the 'perch effect'. To study this effect at Ngel Nyaki I determine which bird species enter the grassland and explore how the characteristics of these trees influence bird behaviour. By relating this behaviour to seedling establishment under the trees I hope to better understand the process of bird seed-dispersal from forest into grassland, and how these isolated trees can influence the establishment of other forest tree species.

The specific questions I am investigating are:

- What bird species are utilising the grassland habitat?
- Do birds prefer certain tree characteristics when choosing isolated trees on which to perch?
- Is seedling establishment under isolated trees related to bird visitations or to tree characteristics?

2.2 Methods

Study area

This study was carried out in regenerating grassland in and around Ngel Nyaki forest (see General Introduction for an in-depth discussion of this area). Three of the fenced grassland sites were used for this trial (Figure 2.1).

Figure 2.1: Map of Ngel Nyaki forest with study sites outlined. Left to right: site 3, site 2, site 1. Adapted from Google Maps (2014).

2.2.1 Experimental design

Bird observations

At each of the three sites, six focal trees were chosen for observations. All the trees were fully isolated from the forest edge (i.e. had degraded grassland between them and the edge) although some were within small patches of other trees. These focal trees were chosen to provide a general representation

of the trees at the site with a range of species, heights, canopy sizes, and distances from the forest edge.

Observations were carried out at in the morning (0630-0830hrs) and late afternoon (1530-1730) to coincide with peak bird activity times. One round of observations took nine days during which time all trees were observed twice – once in the morning and once in the afternoon. Observations were repeated three times over the dry season: late November 2013 (trial 1), early January 2014 (trial 2), and February 2014 (trial 3). During each two hour sampling period two observers watched two different trees using binoculars, so that a total of 216 people hours of observations were collected. We sat on the ground or rocks approximately 20m away from the trees being observed. We did not appear to affect visitation rates as birds would frequently perch on trees nearer to us than the focal trees. Every bird that landed on the observed tree was identified to the lowest taxonomic division possible, or failing that, to feeding guild based on beak shape. The duration of the visit was recorded in seconds. If a bird temporarily left to catch an insect, its return was not recorded as a separate visit (Sheldon & Nadkarni, 2013).

As well as the focal tree, the area in an 8m radius around it was also observed and the number of birds that flew through the area or perched on trees within that area (other than the focal tree) was also recorded.

Tree characteristics

Tree characteristics were recorded for the 18 focal trees (see Appendix 6.1). For each tree we recorded: i) species, ii) diameter at breast height (DBH), iii) height, iv) canopy area, v) canopy cover of surrounding area (measure of isolation), vi) whether it was flowering or fruiting at any of the observation times, vii) distance of the tree from the forest edge (DFFE), viii) canopy density, ix) type of fruit the tree produces – fleshy or non-fleshy.

Tree circumference was measured in cm at 1.3m above the ground and then divided by π to get DBH. Height for taller trees was estimated to the nearest half metre based on known lengths of sticks we had with us; trees short enough that we could get to the top were measured directly with a tape measure. Canopy area was measured by estimating the area of ground that was covered by the tree. This was calculated by measuring the diameter of the canopy in two directions, then calculating total coverage. The degree of isolation is an estimate of the area covered by the canopy of a different tree or shrub (over 1.3m tall) within a 8m radius of the focal tree (approx. area 201m^2) (Sheldon & Nadkarni, 2013). This was achieved by measuring the diameter of the canopies of the surrounding trees and then calculating the total area covered. As the grassland sites are quite small, an 8m radius was used as I believe it is as large an area as possible at these sites for the behaviour of the birds to still be associated with the focal tree. The distance to the forest edge was measured as the distance from the trunk of the tree to the start of the canopy at the nearest forest edge, this was done with a tape measure. Canopy density was a factor of 1 to 4 where 1 had no or very few leaves, and 4 was a canopy you could not see through. Photos of the trees were taken and compared to each other to ensure trees with similar canopy densities were allocated to the same level (see Appendix 6.2). The type of fruit produced was based on information from the NMPF field assistants, and an internet search of the species.

Bird identification

The 'Field Guide to the Birds of Western Africa' (Borrow & Demey, 2008) was used for bird identification and to establish average sizes and normal habitat preferences. Species diets were taken from "The Birds of Africa" volumes 1-7 (Brown et al., 1982; Urban et al., 1986; Fry et al., 1988; Keith et al., 1992; Fry et al., 1997; Fry et al., 2000; Fry & Keith, 2004)

Charles Nsor was mist-netting for his study in some of my sites during days that I was not doing observations. I accompanied him approximately six times to take photos of those birds that were captured to help me with future species identification.

Seedling density

I recorded every seedling (<1m), by species, that was discovered under the canopies of the 18 focal trees. Within the same three sites I took six 2m x 2m quadrats in the grassland (not under a tree). All seedlings within these areas were counted to give an average seedling density for the open grassland.

2.2.2 Statistical analysis

Analysis was carried out in R 3.0.3 (R Core Team, 2014) with the packages 'car' (Fox & Weisberg, 2011), 'multcomp' (Hothorn et al., 2008) and 'lme4' (Bates et al., 2014). Within each trial the morning and afternoon observation periods were combined for each tree, to give total bird visitation numbers per tree, per trial.

Tree characteristics

The relationship between tree characteristics and the number of bird visitations was analysed using mixed effects models (to allow the inclusion of random effects) with a poisson error distribution (for count data). My response variable was the number of bird visits. Fixed effects included height, DFFE, DBH, canopy area, canopy density, and the presence/absence of a food source. Random effects included tree ID, site, and trial number to correct for pseudo-replication, and observation number to correct for over-dispersion (Elston et al., 2001). Separate linear models with bird visits as the response variable and isolation as the fixed effect were used to explore the influence that tree 7 had in the significant effect of isolation that the first fixed effects models showed. Leverage tests confirmed that the influence this point had on the model was significant and that without this point there was no significant relationship. As a result isolation levels were taken to be non-significant and excluded from this analysis (for further discussion see Appendix 6.3).

The relationship between tree characteristics and the average time spent perching on the tree by bird visitors was analysed using linear mixed effects models (to allow inclusion of random effects) with a gamma error distribution. My response variable was the average time spent on the tree by birds. Fixed

effects included height, DFFE, DBH, canopy area, canopy density, isolation and the presence/absence of a food supply. Random effects included tree ID, site, and trial number to correct for pseudo-replication. Points for trees 10 and 14 from trial 2 were excluded from this analysis as no birds were recorded visiting during these times.

A type 2 Anova (car package) was used because it does not take into account the order in which factors are added into/taken out of the model. This was important due to the non-orthogonal design of the experiment. I used the Anova output to remove the factor with the most non-significant effect and checked this with Akaike Information Criteria (AIC) to choose the best fit model (Crawley, 2012). I also compared models using Anova. When models were not significantly different the best-fit model was chosen based on parsimony (ie. fewest factors included).

Effect of canopy cover on bird behaviour

These analyses used the data collected on numbers of birds flying through or perching in the area around the focal tree (8m radius circle = approximately 201m^2). Total canopy area (m^2) within this circle = the canopy area of the focal tree plus the canopy area of all other trees in the circle (isolation data). Total birds in the area = the number of birds perching on the focal tree, flying through the area and perching in the area combined. In order to determine the effect of canopy cover on the number of birds in the area a linear mixed model with a poisson distribution was used. The total number of birds in the area was the dependent variable, total canopy cover was the independent variable, and site, tree ID, and trial were random variables.

To test the effect of canopy cover on the proportion of birds stopping to perch on a tree was calculated with a binomial linear mixed model. The number of birds perching = the number of birds perching on the focal tree plus the number of birds perching in the area. Those that were recorded flying through the area were ‘not perching’. These were combined into a ‘response’ variable, while total canopy cover was the independent variable.

A binomial linear mixed model was also used to test for the relationship between the proportion of the canopy area taken up by the focal tree, and the proportion of birds that land on that tree compared to elsewhere in the area. Then number of birds landing on the focal tree, and those landing elsewhere were combined into a 'response' variable. The proportion of the total canopy taken up by the focal tree was the independent variable and was calculated as the canopy area of focal tree divided by the total canopy cover in the area multiplied by 100.

Seedlings

A series of poisson linear mixed models were constructed to look at the relationships between seedlings and bird visits. All had site as a random variable to account for pseudoreplication, and tree number to account for overdispersion. The four GLMs were i) total seedling number (dependent variable) and number of bird visits (independent variable), ii) total seedling number (dependent variable) and average bird stay length (independent variable), iii) seedling density (dependent variable) and number of bird visits (independent variable), and iv) seedling density (dependent variable) and average bird stay length (independent variable). Two poisson linear mixed models were also used to test for a relationship between whether or not the focal tree produces fleshy fruit (dependent variable), and the number and density of seedlings found (independent variable).

Multivariate detrended correspondence analysis (DCA) using the program CANOCO (Braak & Šmilauer, 2002) was used to detect the underlying structure of the seedling community data, and convert tree characteristics to 'principal components' to help explain the observed patterns in the data set. The first principal component accounts for as much of the variability in the data as possible and each component after has the highest variance possible after the preceding components have been taken into account. This shows the level of influence each of these tree characteristics has on the seedling community below the tree's canopy. DCA provides an ordination based on the species composition and total seedling numbers found under each tree, on each of the dominant gradients so trees that are closer together on the ordination are more similar in terms of the seedling community (numbers and species of seedlings) found under them.

2.3 Results

Species observed – habitat, diet, and size

A total of 59 different bird species were observed in the grassland areas around the forest edge from November 2013 to February 2014 (see Appendix 6.4). Seven of these species (12%) are primarily frugivorous – the Cameroon Olive Pigeon (*Columba sjostedti),* African Green Pigeon *(Treron calvus),* Common Bulbul (*Pycnonotus barbatus),* Double-toothed Barbet *(Lybius bidentatus),* Speckled Mousebird (*Colius striatus),* Yellow-rumped Tinkerbird *(Pogoniulus bilineatus),* and Little Greenbul (*Andropadus virens*). Fruits make up a minor part of the diets of another 17 species (29%) while the remaining 35 species (59%) included no fruit in their diets (Fig. 2.2a) . Thirteen of the species (22%) observed were primarily forest species. Thirty-one of the species (52%) prefer various savanna and wooded habitats where there is a mixture of grass and trees. Eleven species (19%) are grassland species, while four (7%) are forest edge species (Fig. 2.2b). Most birds observed were small with over two thirds of them being between 10 and 20cm long. Only seven of the species are over 25cm long, and of these only two – the African Green Pigeon and the Cameroon Olive Pigeon – are primarily frugivores.

I recorded 1362 observations of birds landing on focal trees. Birds used focal trees for a range of activities including feeding, calling, and resting. 14% of the recorded visits were by the seven species of primary frugivores, although 88% of these were Common Bulbul. Sunbirds of all species (Variable, Northern Double-collared, Orange-tufted, and Splendid) made up 32% of the total visits to focal trees (Fig. 2.2c). There were a lot of birds that I could not identify exactly or with confidence, but small grey/green/brown birds (including *Sylvia borin, Phylloscopus trochilus, Melaenornis pallidus*), made up 25% of the total observations. These birds are assumed to be warblers, flycatchers or similar species which are primarily insectivorous but will also eat small fruits and berries.

Other frugivores were observed in the grassland areas during this time but were not specifically recorded. These species included Tantalus Monkeys *(Chlorocebus tantalus)*, Olive Baboons (*Papio anubis)*, Blue Duiker (*Philantomba monticola*), African Civet (*Civettictis civetta)*, and Bats.

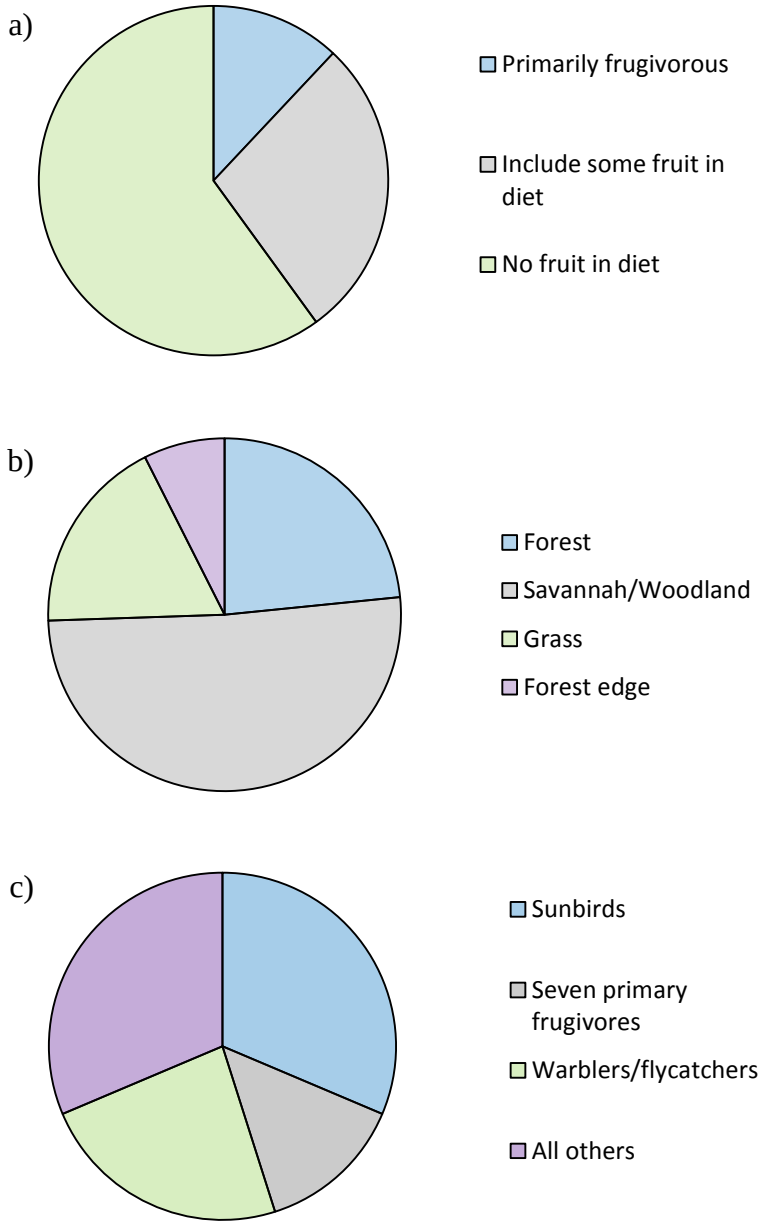


Figure 2.2 Visual representations of: a) the total observed species (n = 59) divided by diet type, b) total observed species (n = 59) divided by preferred habitat type, c) total observed visits to focal trees (n = 1362) divided by each of the most common groups.

Effect of tree characteristics on visitation number

Only two of the measured tree characteristics had a significant effect on the number of bird visits to a tree (Table 2.1). Larger canopy areas had, in general, more bird visitations ($p = 0.002$) (Fig. 2.3), as did those trees that were either in flower or had fruit ($p = 0.011$) (Fig. 2.4). Height, DBH, canopy density, and distance from the forest edge had no significant effect. The degree of isolation had no significant effect on the number of bird visits when the outlying data point for tree 7 was removed (see Appendix 6.3).

Table 2.1 Results from the binomial linear mixed model, calculating the effects of tree characteristics on the number of birds observed visiting focal trees. Stars denote significant effects at $p = 0.05$.

Source of Variation	Chi-squared	DF	P value
Height	3.394	1	0.065
Canopy Area	9.159	1	0.002 *
DBH	0.748	1	0.387
Canopy Density	0.975	1	0.323
Distance from Forest	0.0001	1	0.992
Fruit/flower presence	6.5186	1	0.011 *

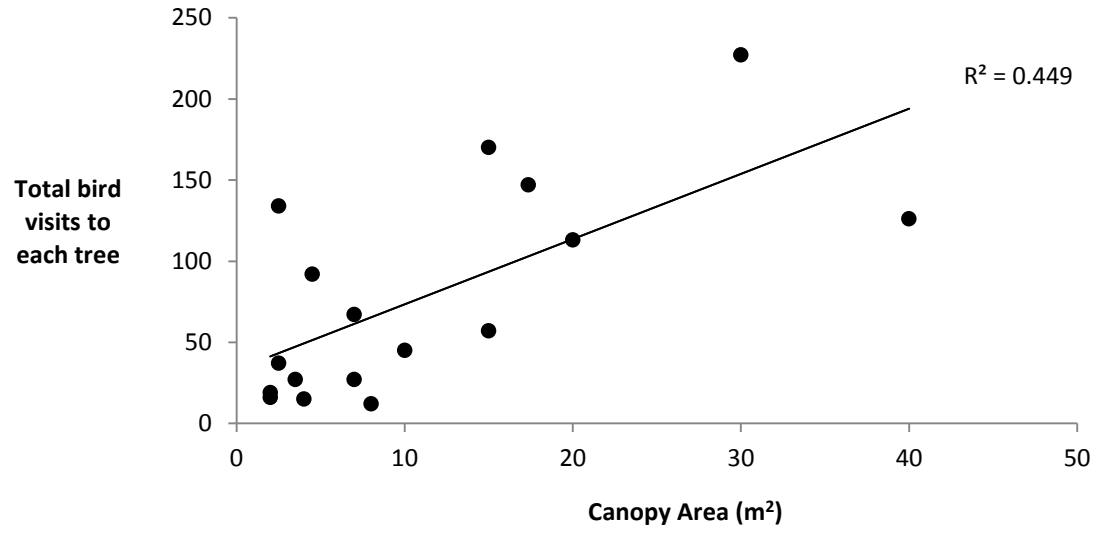


Figure 2.3 Relationship between the canopy area of the focal tree (m^2), and the total number of bird visits to that tree (combined over all observation periods) ($p = 0.002$). Each point represents one focal tree.

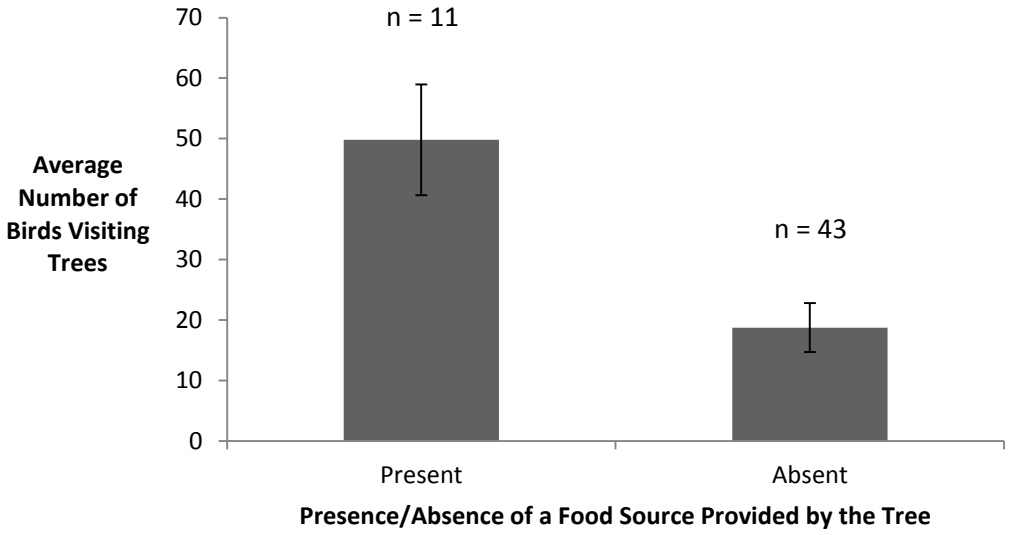


Figure 2.4 Average number of birds visiting a focal tree (per trial) based on whether or not the tree was providing a food source (either flowers of fruit) during that trial period (p = 0.011). Error bars are ± 1 SE.

Effect of tree characteristics on visitation length

The presence of a food source (either flowers or fruit) on a tree was positively related to the period of time spent on a tree by bird visitors (p = 0.035) (Table 2.2, Fig 2.5). No other factors (canopy area, canopy density, height, distance from forest edge, DBH, or isolation) had a significant effect.

Table 2.2 Results from linear mixed model calculating the effect of tree characteristics on the average length of time birds stayed on a tree. Stars denote significant effects at p = 0.05.

Source of Variation	Chi-Squared	DF	P value
Height	0.686	1	0.408
Canopy Area	0.023	1	0.879
Canopy Density	1.106	1	0.293
Distance from Forest	0.147	1	0.701
DBH	0.374	1	0.541
Isolation	0.327	1	0.568
Fruit/Flower Presence	4.453	1	0.035 *

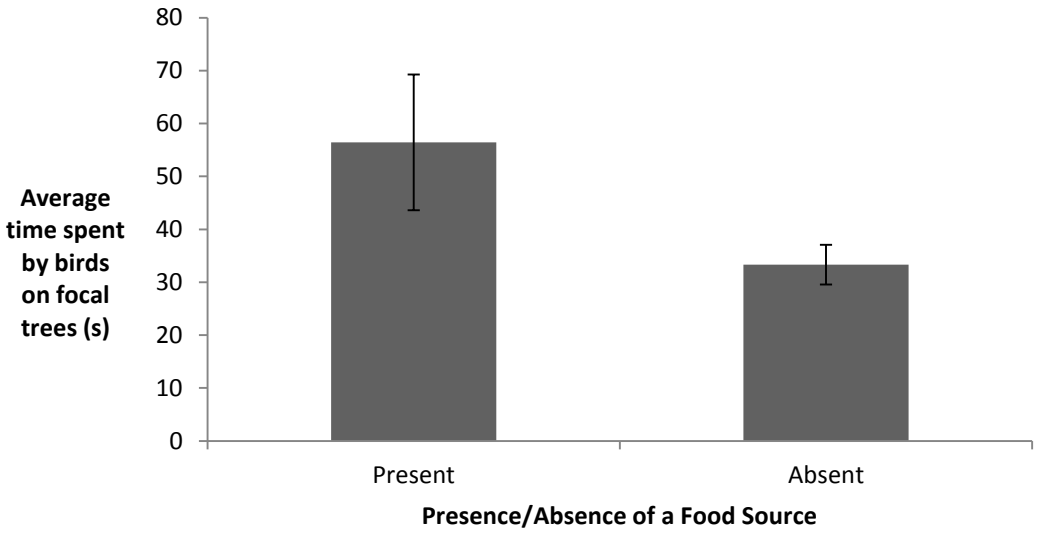


Figure 2.5 Average time (s) that birds spent in each focal tree in each trial based on whether or not the tree was providing a food source (either flowers of fruit) during that trial period (p = 0.035). Error bars are ± 1 SE.

Effect of canopy cover on bird behaviour in predominantly grassland areas.

The number of birds that were observed within the area around a focal tree (circle of 8m radius = 201m^2), both flying through and perching, showed a positive relationship with the percentage of that area under canopy cover (p = 0.012, df = 1, ChiSq = 6.24) (Fig. 2.6). Also, the greater the percentage of canopy cover within the area, the higher the proportion of birds that stop to perch instead of flying straight through (p = 0.038, df = 1, ChiSq = 4.28) (Fig. 2.7). The proportion of birds that stop on the focal tree instead of elsewhere in the area increases with an increasing proportion of the total canopy area that is provided by that focal tree (p = 0.014, df = 1, ChiSq = 6.01) (Fig. 2.8), although this is not a 1:1 relationship.

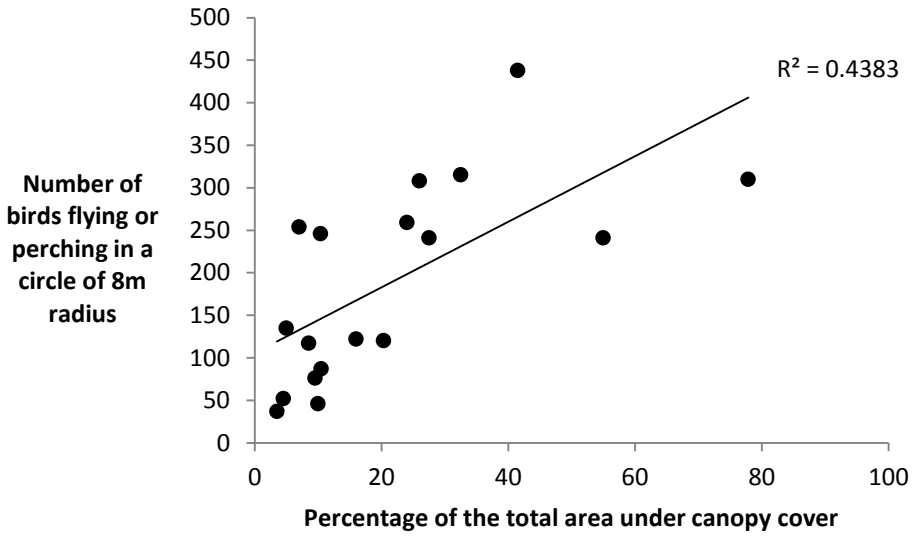


Figure 2.6 The number of birds that were observed in an 8m radius of the focal tree, either perching in or flying through the area, in relation to the percentage of that area that was covered by the canopy of any tree over 1.3m tall (p = 0.012).

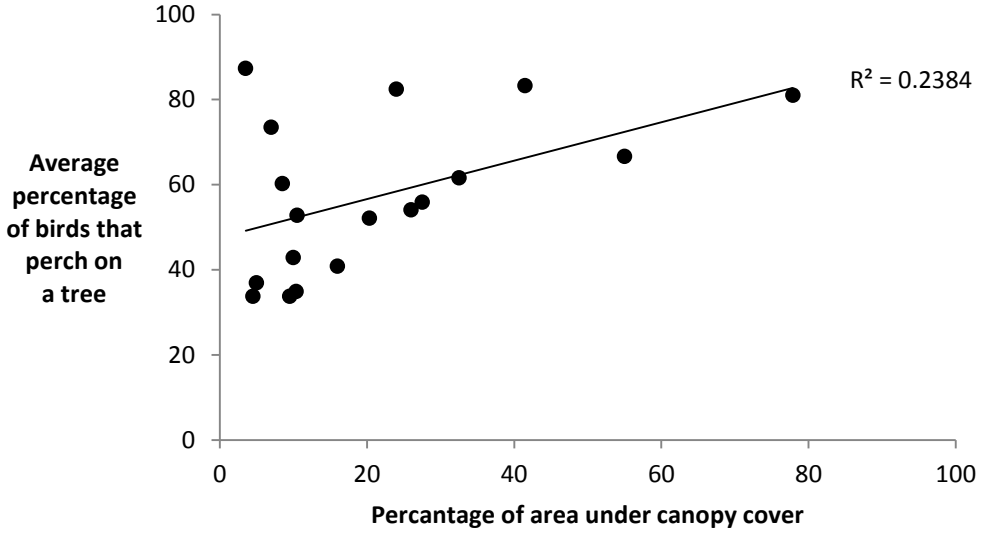


Figure 2.7 Of the birds that were observed within an 8m radius of the focal tree, the average percentage of them that stopped to perch in the area, compared to the percentage of that area that was under canopy cover (p = 0.038).

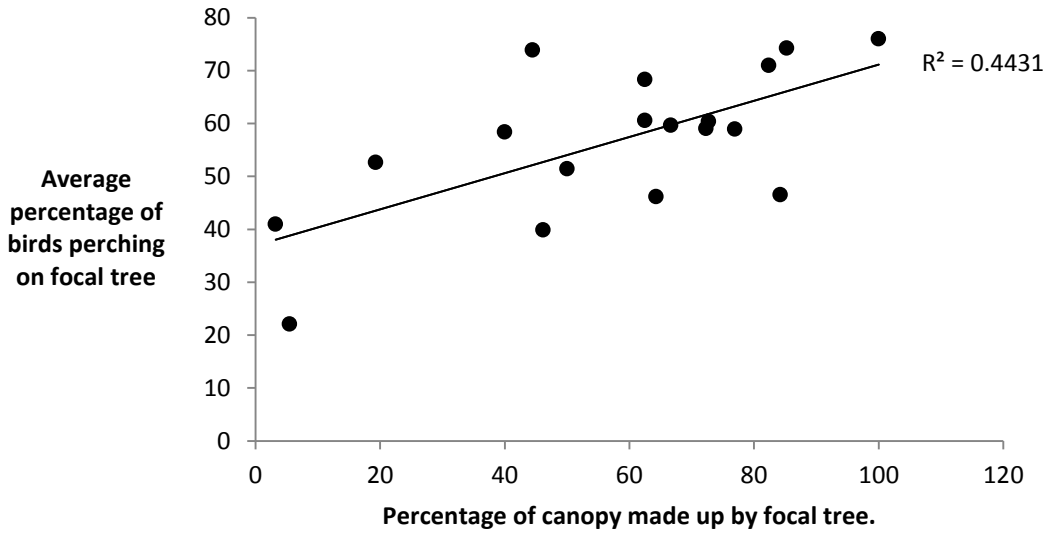


Figure 2.8 Of the birds that were observed perching in an 8m radius of the focal tree, the average percentage of them that landed on the focal tree, in relation to the percentage of the canopy cover in that area that was made up by the focal tree (p = 0.014).

Effect of birds visits on seedling numbers

A total of 1460 seedlings (<1m tall) were recorded under the canopies of the 18 focal trees (see Appendix 6.5 for table). Seedling numbers ranged from four under Tree 17 to 388 under Tree 8. Seedling densities ranged from one per m^2 to 55 per m^2. Seedling density for open grassland areas (not under trees) was 0.2 per m^2. Twenty different species were recorded from 15 families (Fig 2.9) (see Appendix 6.6 for full table). Only 5% of the seedlings were found under conspecific trees meaning at least 95% must have been dispersed from elsewhere. Thirteen of the seedling species have vertebrate dispersed seeds, and these 13 species account for over 98% of the total seedlings found. 24% of the seedlings found were from six grassland or savannah species. Nine of the species were forest edge species accounting for 74% of the seedlings, and the remaining five species, or 2% of individuals, were species from the forest core.

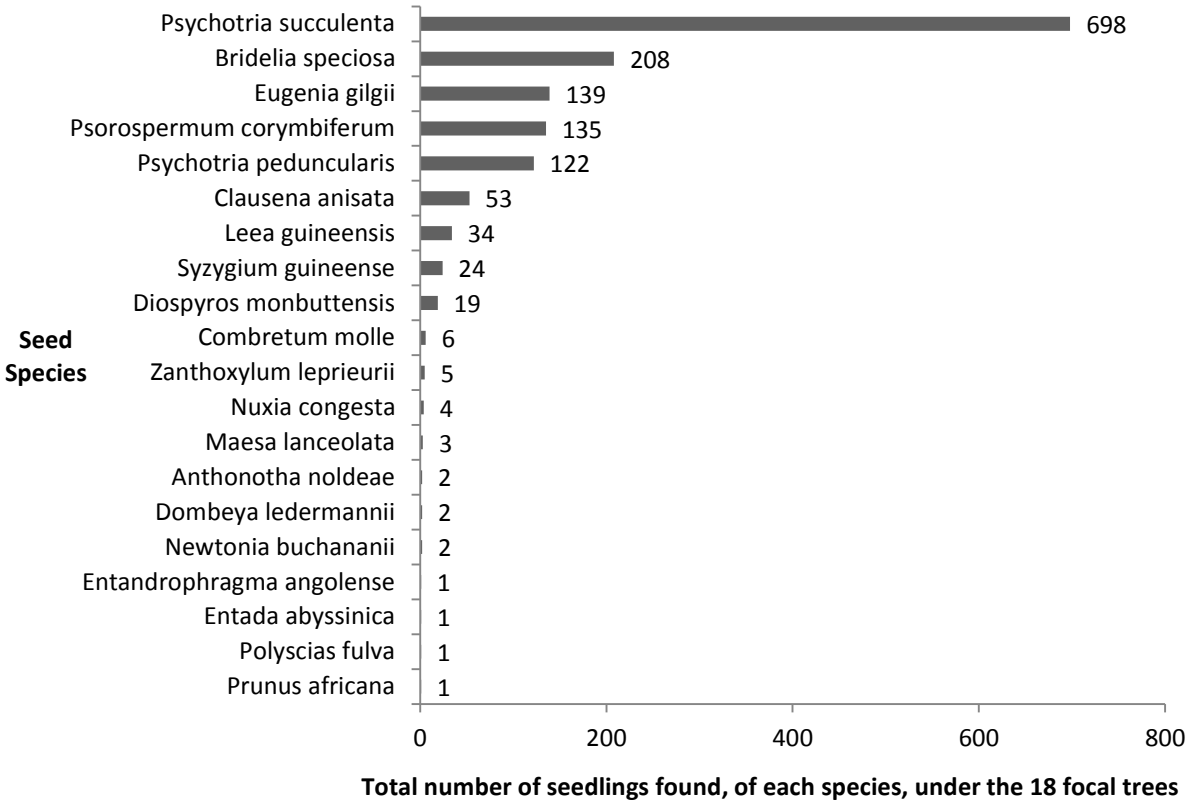


Figure 2.9 Total number of seedlings from each species that was found under the canopies of the 18 focal trees.

The total number of birds visiting each tree was significantly positively correlated with the number of seedlings found below that tree ($p < 0.000$, df = 1, ChiSq = 19.191) (Fig. 2.10) and with the density of those seedlings ($p = 0.030$, df = 1, ChiSq = 4.7025). The average length of bird visits to a focal tree was not significantly correlated with either total seedling numbers ($p = 0.271$) or seedling densities ($p = 0.141$). Whether or not the focal tree produced fleshy fruit had no significant effect on either the total number of seedlings, or seedling density, below the canopies of the trees ($p = 0.555$ and $p = 0.427$ respectively).

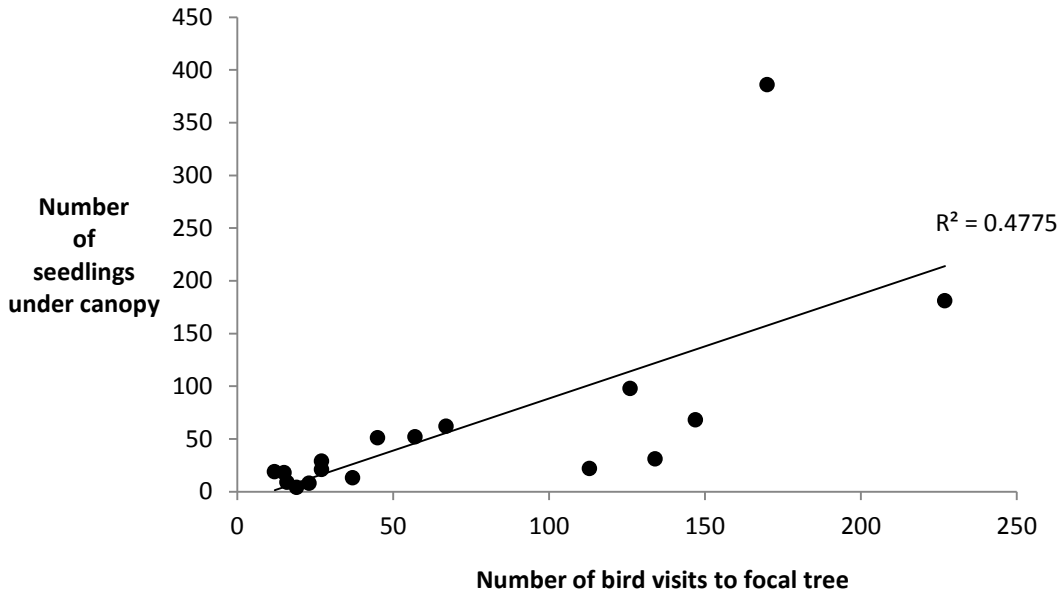


Figure 2.10 Relationship between the number of bird visitations to a focal tree and the number of seedlings found underneath the canopy of that tree ($p < 0.000$).

Effect of tree characteristics on seedling numbers

Axis 1 of the ordination explains that 32.5% of the variation in the floristic data is strongly correlated with both the distance of the tree from the forest edge and the tree's DBH (Fig. 2.11a). The second ordination axis only explains 9.3% of the total variation and isn't strongly correlated with any measured tree characteristics. There appears to be some sorting of the seedling community in terms of the tree species they occur under, with this occurring especially along ordination axis 2. *C. molle* trees have higher values on axis 2 than *B. speciosa* and *N. congesta*, suggesting that tree species does have some influence on seedling composition. As only one or two individuals were present for the other tree species, it is not possible to assess any patterns with these, although the two *Syzygium guineense* trees had very different scores on axis 2 of the ordination. Seedling communities seem to be different in the three sites, along both ordination axes (Fig. 2.11b).

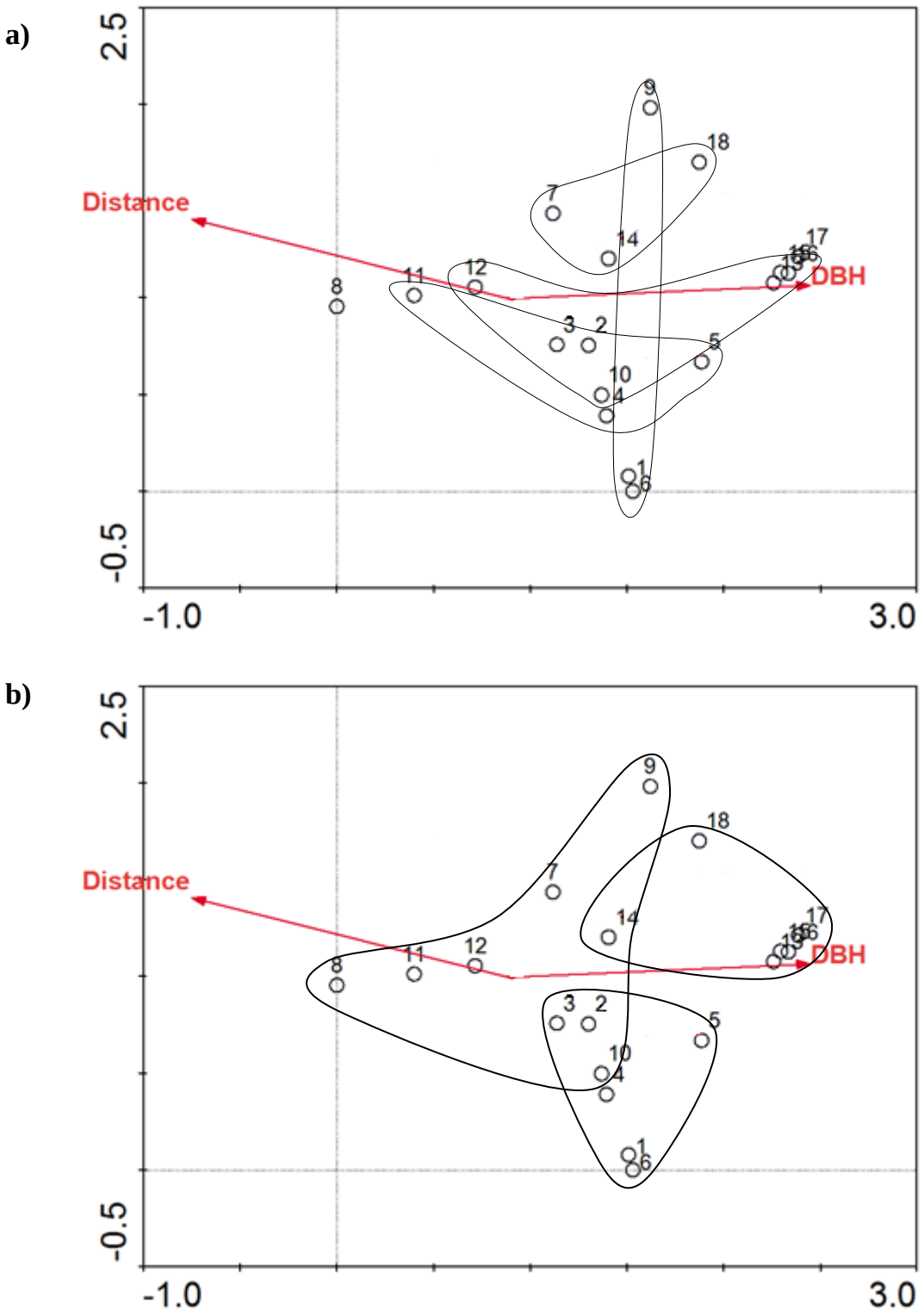


Figure 2.11 Axes 1 and 2 of the DCA ordination. Trees that are closer together are more similar in both seedling number and species makeup. The direction of the two tree characteristics that are significant. a) four of the tree species superimposed, b) trees are grouped by site.

2.4 Discussion

2.4.1 Bird usage of trees and the effect on seedling numbers

What bird species are utilising the grassland habitat?

The 59 bird species observed in the grassland habitat is a positive sign that this system is providing a useable habitat for at least a proportion of the bird species in the reserve. Without data about all the species of bird present at Ngel Nyaki I am unable to say absolutely whether the species using the grassland tend to be smaller in body size than those in the forest, or whether the ratio of frugivores to granivores and insectivores in this habitat is different. However there are some groups of large frugivores, such as hornbills and turacos, which are known to be in the forest but that were not observed in the grassland. Body size is important for frugivores as it is linked to gape size which in turn limits the size of fruits (and therefore seeds) that the bird is able to consume (Wheelwright, 1985). The lack of these large birds leaving the forest has the potential to limit the dispersal of larger seeded tree species into the grassland. Moreover, though a wide range of species are necessary for a functioning system, only the frugivores are directly contributing to seed rain. Of the bird species observed 40% include fruit as part of their diet, and any management practices that increase the numbers of frugivorous individuals or species will be beneficial for regeneration. With the current data it is not possible to determine what percentage of forest birds visit grassland but this is likely to be low, as was found by Da Silva (1996) in the Amazon. Only 22% of the birds species observed were primarily forest dwelling birds, yet these are the species that bring seeds from the core forest into the grassland. However frugivores that prefer wooded or open habitats will still disperse seeds from other regenerating areas where the canopy is not so thick, so still play a role in seed dispersal through the degraded habitats. Other studies have found that the seeds dispersed into degraded areas tend to be from other degraded areas (Duncan & Chapman, 1999; Graham & Page, 2012) which is probably due to dispersers staying in the one habitat type.

The mammal dispersers that were seen during this study can carry large seeds and from long distances away, due to their size and travel distances, which potentially makes them very important dispersers despite their relative lack of numbers in the grassland (Kunz & Linsenmair, 2008; Agmen et al., 2010). However their abundance and behaviours were not directly assessed in this study.

Do birds prefer certain tree characteristics when choosing where to perch?

Individual trees that were preferred as perching places had both higher visitor numbers and longer average stay periods. This implies that characteristics the birds are using in their decision to land on trees are similar to those that influence how long they stay there.

Trees with larger canopy areas had higher visitation rate. This could be either because they provide more area for perching and therefore have more birds landing in total, or because birds deliberately choose larger trees. Larger trees may attract more birds due to greater food availability (Fretz, 2002), or because greater areas inside the canopy reduce the vulnerability to predators (Kullberg, 1998). The availability of food also had a significant effect on the number of visitors to a tree as birds landed to forage. Not all the visits to flowering trees appeared to be for nectar, many birds were observed taking insects from on and around the flowers. It is hard to tell what the effect of fruiting trees is as there was only one tree that had fruit over the observation periods. Some studies have found grassland trees are preferred during low fruiting periods when frugivores are forced to travel into less preferred environments (Herrera & García, 2009), while others found most birds ventured into the grassland during high fruit times when these trees are more appealing (Da Silva et al., 1996).

The availability of a food source was the only tree characteristic to have a significant effect on the average length of time that an individual bird stayed on a tree once it landed. This coincides with optimal foraging models that state that feeding birds should stay in a patch with an available food source for longer periods of time than patches with little or no food (Senft et al., 1987).

I found no relationship between the distance of the tree from the forest edge and the numbers of bird visitors. This lack of pattern has been found in some studies (Sheldon & Nadkarni, 2013) while others have shown positive (Lasky & Keitt, 2012) and negative relationships (Da Silva et al., 1996). This lack of relationship I found may be because all my focal trees were within 90m from the forest edge, and other studies have shown no relationship in bird numbers at greater distances than this (Eshiamwata et al., 2006). Sites 2 and 3 had the largest distances to the forest edge but had relatively high levels of structural habitat diversity which may reduce the effect of distance by creating corridors and series of tree islands out into the grassland. Alternatively there may be a change in the species of visitors along the distance gradient that was not picked up in this study i.e. the trees further out were visited by grassland species while the ones close to the edge had more forest species (Lasky & Keitt, 2012).

Effect of canopy cover on bird usage of small areas

I found no effect of the degree of isolation of a focal tree on the number of birds visiting, seemingly implying that birds are insensitive to the isolation of trees, as found in eastern Amazonia (Lasky & Keitt, 2012). However I can only say that this is true in this system if the surrounding canopy cover is less than $30m^2$ in the $201m^2$ around that focal tree. I only had one tree with a surrounding canopy area higher than $30m^2$ and without more it is impossible to know if the relationship that was found at these higher levels is a true biological pattern or if it is simply a relic of this data set. If this experiment was to be continued and extended then I would recommend more trees with higher canopy cover surrounding them to be included to further inspect this pattern.

I found that the total number of birds in a small area ($201m^2$), as well as the percentage of birds that stopped on a tree while in that area, were both positively related to the total amount of canopy cover. However if the focal tree was surrounded by many other trees (high canopy cover) then fewer birds landed on that focal tree. This study suggests that canopy cover provides an important structural element for attracting birds into degraded grassland and that only observing a single tree can give a false representation of bird behaviours. As higher levels of canopy cover provide more options for

birds of where to perch, the visitations to the focal tree are lower (Fink et al., 2009; DeMars et al., 2010). The relationship I found between the percentage of canopy cover and the percentage of birds perching on the focal tree was not absolute as smaller birds sometimes perched on grass, rocks and twigs that were not classed as 'Canopy'.

Is seedling establishment related to bird visitations or to tree characteristics?

Seedling densities under trees were much higher than in open grassland and I found a significant positive relationship between the number of birds observed visiting a tree, and the number of seedlings below its canopy. This is consistent with the hypothesis that more visiting birds leads to an increase in seed rain which in turn increases seedling numbers (the "Perch Effect") (Cavallero et al., 2013). This further emphasises the relationships between disperser movements, seed dispersal and plant succession in these grassland habitats, similar to studies in the Amazon (Da Silva et al., 1996) and United States (McDonnell & Stiles, 1983).

Only 2% of the seedlings found were of core forest species. This suggests that these species are more microsite or dispersal limited in grassland than species of other successional stages. This will lead to the developing secondary forest being much sparser in these species than the original forest. As the secondary forest matures the new environment may be more conducive to the dispersal and germination of these species, raising their numbers. Alternatively active management practices may be required to create the desired species makeup in these regenerating areas.

The ordination shows that the makeup of the seedling community is strongly associated with the distance from the forest edge and tree DBH. If this is indicative of a relationship between seedling number and the distance from the forest edge then this does not appear to be related to the observed bird behaviours as no similar relationship was found. However the ordination also takes into account the species makeup of the seedlings, so this pattern may be due to the differential dispersal and survival of seedling species at increasing distances from the forest edge, as found by Barnes and Chapman (2014) at the same forest. DBH is related to height and canopy area as measures of tree size,

so possibly the higher bird visitations at trees with larger canopies is related to the higher seedling numbers under trees with larger DBHs. I found very different seedling communities under trees in each of the three sites which is possibly due to the range of adult trees (seed sources) in the forest bordering each site governing which species get dispersed into the grassland.

The dispersal method of the focal tree's seeds did not have a significant effect on seedling densities which was unexpected, since it could be assumed that fleshy fruited trees would attract more frugivores that would then deposit seeds from other trees (Hamann & Curio, 1999). A larger sample size may show up a small but significant difference as I only took data from 18 trees. Alternatively, because many of the bird species observed in this trial are primarily insectivores that consume some fruit, they may be attracted to trees for other reasons throughout the year, such as the presence of flowers or insects, and yet still deposit seeds.

2.4.2 Limitations of this trial and future directions

Due to restrictions in the field season that was available to me, the three trials for this study were all carried out during three months of the dry season. Monthly observations for a whole year instead of just the dry season would further enhance our knowledge of how these trees and the grassland areas are used throughout the year. It would allow each of the focal trees to have both flowers and fruit during at least one of the observation periods so the effect of these food sources can be fully understood. It would also allow for different bird species and behaviours throughout the year; many of the birds found in West Africa are migrants (Borrow & Demey, 2008) so the observed species will change depending on the season of observations.

Only studying 18 focal trees may have restricted my ability to find small patterns between tree characteristics and bird behaviours due to many confounding factors. Continuing this study on a larger scale would provide more data for accurately analysing these effects, particularity that of isolation.

The large over dispersion found in the data also implies that there were factors that controlled bird spatial distributions that I did not measure, for example tree species or insect densities (Fretz, 2002). Measuring seedling communities under more focal trees could also help to bring into focus some of the factors governing this. Seedling survival is not just dependent on seed rain but also lots of other factors such as microsite conditions (Reid & Holl, 2013). Installing seed traps under the focal trees to look at the seed rain being dropped by perching birds would also help to fill in this intermediate step and allow for inferences about the filtering processes between seed rain and seedling establishment. Although every effort was made to see and record every bird that visited the focal trees, some individuals may have been missed as some trees were in positions where it was harder to see them from all directions, and trees with higher canopy covers also made viewing more difficult. Many individual birds were not able to be identified in the field. Having the ability to more accurately identify the species of visiting birds, either by carrying out mist-netting, or by having a bird expert carry out the study, would provide more analysable data to use to look for small-scale patterns. For instance analyses involving the effects tree characteristics have on specific bird species of guilds would become possible (for example Lasky & Keitt, 2012).

2.5 Conclusions

This study was the first at this forest that examined the behaviour of birds within the regenerating areas around Ngel Nyaki forest. The total of 59 species observed was a positive sign that these regenerating habitats are being used by bird species. Although currently grazed pasture was not explicitly surveyed it appeared many of the species observed were only in the fenced off grassland and not in the pasture. Also many of the birds observed are grassland or savanna birds. This shows that this regenerating landscape is an important system in its own right, not just as a transition to forest. It is concerning that some of the larger forest birds do not appear to use the grassland habitat but this is not unexpected. Seed dispersal of early successional trees from the smaller birds will hopefully, over time, create a secondary forest that is more likely to be used by a larger range of species (Yarranton & Morrison, 1974).

Birds do choose certain trees over others based on some of the characteristics that I measured, and probably others that I didn't. There is a general preference for larger trees and areas with higher levels of canopy cover, implying that continued regeneration will further increase bird use of these areas. Planting fast growing trees with wide canopies, and planting trees in patches will also promote bird visitation.

I found evidence of the perch effect in this system due to the strong connection between bird visits and seedling numbers. The high percentage of seedlings that are a different species to the adult is a strong indicator that dispersal is occurring at reasonable levels in these grasslands and is a positive sign for passive regeneration.

Chapter 3: Post-Dispersal Seed Predation

Interactive Effects of Seed Species, Habitat, and Predation Guild

3.1 Introduction

3.1.1 Post-dispersal seed predation

Seed predation in regenerating systems

Post-dispersal seed predation is a major source of seed mortality in many tree species (Blate et al., 1998) and can be a key post-dispersal filter limiting seed survival (Myster, 2004). Predation rates in tropical systems are particularly high, often with over 60% removal in the first 30 days (Hammond, 1995; Obeso & Fernández-Calvo, 2003; Barberá et al., 2006; Salazar et al., 2012). Predation levels tend to be highly variable even within a system (Holl & Lulow, 1997), so general rules are hard to establish. Seed species, year, site, habitat, microhabitat, predator species, seed density, and season have all been found to influence predation rates (Willson & Whelan, 1990; Whelan et al., 1991; Hulme, 1994; Holl & Lulow, 1997; García et al., 2007; Pérez-Ramos & Marañón, 2008). Also, there are often interactive effects between these factors (González-Rodríguez & Villar, 2012; Maron et al., 2012) leading to complicated patterns in both predation rates and final seed distribution.

In an established forest, seed predation is an important process, sustaining granivore populations and helping to maintain plant diversity (Hulme, 1998b; Paine & Beck, 2007; Herrera & García, 2009). However in regenerating systems this balance has often been disrupted, and seed predation is considered a factor which slows and negatively impacts regeneration. Seed predation will only affect the recruitment of seedlings if that species is already seed limited in that area, i.e. fewer seeds are dispersed to the area than would be able to germinate and survive (Calviño-Cancela, 2007; Denham, 2008). In regenerating areas dispersal is often limited so the predation of those seeds that are dispersed significantly impacts on regeneration success. Moreover any variation in predation rates among seed species (Barberá et al., 2006) can lead to the selective recruitment of some species (García et al., 2005), which may in turn affect the composition and population dynamics of regenerating areas (Holl & Lulow, 1997; Blate et al., 1998; Shen et al., 2008).

Effect of predator species

High levels of vertebrate predation have been found in systems worldwide (Hulme, 1994), but ants have also been shown to be a major predator in tropical forests and arid ecosystems (Hulme, 1998b). Different predator species can alter the pattern of seed predation due to their occupation of certain habitats and preferences for certain types of seeds (Kelrick et al., 1986; García et al., 2005; Pérez-Ramos & Marañón, 2008).

Habitat effects on seed predation

Many studies have found that habitat has a significant effect on the level of predation (Hammond, 1995; Doust, 2011). Different rates of predation among habitats can often be linked to the foraging patterns and habitat preference of the different predators (Schupp & Frost, 1989; Christianini & Galetti, 2007; Mari et al., 2008). High levels of predation in degraded grassland can limit regeneration through the removal of seed that is dispersed into these areas (Holl et al., 2000; Doust, 2011).

Edge habitats are important to understand as they are where most forest regeneration occurs due to higher seed rain and more favourable abiotic conditions than in adjacent grassland (Holl & Lulow, 1997). Moreover, as forests become fragmented, a greater ratio of forest becomes an edge. Habitat patch size, and the environment that the forest adjoins at the edge can also have impacts on the species present in the edge areas (Jorge & Howe, 2009; Barnes et al., 2014) which may in turn affect predation patterns (Magrach et al., 2011).

Grassland is the most degraded part of the forest/savanna matrix but its effect on predation is not consistent and many contradictory results have been reported. Often predation in grassland is lower than under tree cover (Calviño-Cancela, 2007; Magrach et al., 2011). However some studies have shown that predation decreases with distance from the forest edge (Booman et al., 2009) while in other systems predation increases with distance into the grassland (Craig et al., 2011). These contrasting results are often due to interactive effects with factors such as year, predator species, seed

species, and density dependency making results relatively specific to the system being studied (Willson & Whelan, 1990).

Remnant trees and seed predation

Many granivorous animals use adult trees as foraging tools due to the increased seed rain that is usually found beneath the canopy. The well-known Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971) models this decreasing seed predation, and therefore increasing survival, away from a parent tree (Schupp & Frost, 1989; Shen et al., 2008). In some grassland habitats a similar pattern has been found where seed predation across all species is increased under remnant trees, even if they are not of the same species (Holl & Lulow, 1997; Herrera & García, 2009). Again however, there are contradictory results from some systems where predation was found to be lower under trees as the predators avoided the more open spaces under canopies (Holl & Lulow, 1997).

3.1.2 Aims of this study

High seed predation can negatively impact natural regeneration and restoration attempts. The goal of this study was to quantify the extent of predation of small seeds around Ngel Nyaki forest to better understand the possible impact of predation regeneration patterns. Specifically I looked at the effect of habitat type (core forest, fenced edge, unfenced edge, open grassland, under remnant trees), seed species and predator guild on the levels of seed predation to help answer the following questions:

- Does seed predation vary between habitat types within the reserve area?
- Are seeds below isolated trees in grassland subject to different levels of seed predation than those in the open grassland?
- Does predation guild (vertebrate/invertebrate) have interactive effects with habitat type or seed species in the number of seeds removed?
- What seed characteristics increase the likelihood of them being removed (predated)?

3.2 Methods

Study site

This study was undertaken in and around Ngel Nyaki forest (see General Introduction for an in-depth discussion of this area). Three sites were selected in fenced grassland areas around the border of the forest (Fig. 3.1).

Figure 3.1 Map of Ngel Nyaki with approximate study sites marked. Adapted from Google Maps (2014).

Site 1 and site 2 include four habitat types: 'grassland' sites are old pasture areas that have been fenced-off to protect from cattle grazing and from fire, and grasses and herbs are recovering; 'protected edge' sites are under tree cover at the forest edge adjacent to this fenced-off grassland; 'unprotected edge' is under the tree cover at the forest edge adjacent to unfenced grassland; 'core'

sites are 200m into original forest where they have minimal disturbance. Site 3 is a grassland habitat only.

Study species

Ten tree species were used for this experiment – *Celtis gomphophylla, Croton macrostachyus, Combretum molle, Entandrophragma angolense, Leea guineensis, Newtonia buchananii, Pittosporum viridiflorum, Polyscias fulva, Psychotria peduncularis,* and *Sterculia tragacantha* (see table in Appendix 6.7 for seed characteristics).

For the purposes of this experiment, seed predators found in Ngel Nyaki were divided into two guilds: invertebrates (mainly ants) and vertebrates. I observed at least six species of ant at Ngel Nyaki - although none have been identified at least some are assumed to be seed predators. Vertebrate predators include the African brush-tailed porcupine (*Atherurus africanus)*, squirrels, pouched rats (*Cricetomys sp.)*, and blue duiker (*Cephalophus monticola)*, many of which have been observed predating seeds elsewhere in the forest (Dutton et al., 2014).

3.2.1 Experimental layout

In total three trials were conducted over two consecutive dry seasons – December 2012/January 2013, December 2013/January 2014, and February/March 2014. Four seed species were used for each trial (Table 3.1).

Table 3.1 A summary of the four seed species used for each of the three trials.

Trial	**Species Used**
December 2012 / January 2013	*Leea guineensis, Newtonia buchananii, Pittosporum viridiflorum, Psychotria peduncularis.*
December 2013 / January 2014	*Combretum molle, Croton macrostachyus, Leea guineensis, Psychotria peduncularis,*
February 2014	*Celtis gomphophylla, Entandrophragma angolense, Polyscias fulva, Sterculia tragacantha.*

I was limited in my choice of seed species by which species were fruiting in large enough numbers to collect during the time the study was being carried out. Ripe fruits were collected off three or more parent trees around the edge of the forest (the exact number varied based on the density of fruit that trees in each species produced). Seeds were removed from the fruits by hand, washed, then dried in the sun for one hour. Wings of wind dispersed seeds were left intact.

Seeds were placed out into seed stations (Figure 3.2) on day 0. They were checked again at day 1 and day 5. All seeds were recorded as "present" or "removed". At the day 5 check seeds were removed from the seed stations. After at least one week this was repeated with the same four seed species.

Seed stations

Across all sites and experiments there were 372 seed station locations. At each station two seeds of each species were placed, making a mixed pile of eight seeds in total.

Seed stations were allocated to one of three exclosure types – control (open station where any predator could access the seeds), vertebrate only, and invertebrate only. For control stations, seeds were placed on a small cleared patch of ground, in a slight hollow so the seeds would not roll off or blow away (Fig. 2.2a). Invertebrate only stations consisted of the piles of seeds placed in inverted plastic pottles (2.2b). These pottles had two 1cm by 8cm holes cut at ground level to allow access to ants and other invertebrates. To secure them the lids were nailed to the ground and the pottle was clipped in. For vertebrate only stations (2.2c) the seeds were placed on the ground surrounded by a 'moat' of powder insecticide (Permethrin 0.60%) approximately 1cm wide. Pre-trials established that ants did not cross this barrier to get to a food reward.

Figure 3.2 Seed station set up. a) Control, b) Invertebrate only, c) Vertebrate only.

Transect set-up

Stations were set in lines 5m long, with six seed stations, each 1m apart. Each line contained two stations of each exclosure type in a random order. These lines were spaced along transects in such a way that I was able to run two experiments concurrently. All habitats at site 2 and the core, protected edge and unprotected edge in site 1 had two randomly placed 20m transects in each habitat. Three lines were spaced along each, 10m apart. In site 3 three trees were selected and transects were started at the trunk of these trees. Three lines of seed stations were set up along these transects, under the canopy (0m), 5m out, and 15m out. In order to combine these two layouts the grassland habitat at Site 1 had three transects starting from three trees. Tree 1 and 2 had 25m transects with seed stations at 0m, 5m, 15m, and 25m. Tree 3 had stations at 0m, 5m and 15m. This allowed a replicate of the three trees at site 3, but also the 5m, 15m, and 25m represented open grassland and thus was a replicate of site 2's grassland habitat. All grassland and tree transects were approximately 50m from the forest edge to partially account for the effect of distance into the grassland on predation. A previous study at this site suggested no difference in seed predation levels between 20 and 60m from the edge (Campbell, 2010).

3.2.2 Statistical analysis

Analysis was carried out in R 3.0.3 (R Core Team, 2014) with the packages 'car' (Fox & Weisberg, 2011), 'multcomp' (Hothorn et al., 2008) and 'lme4' (Bates et al., 2014). For all analyses $p < 0.05$ is considered significant. For all models I used the the Anova output to remove the factor with the most non-significant effect and checked this with Akaike Information Criteria (AIC) to choose the best fit model (Crawley, 2012). I also compared models using Anova. When models were not significantly different the best-fit model was chosen based on parsimony (ie. fewest factors included).

Analyses in the temporal change, encounter rate, and total removal sections used the seed stations at sites 1 and 2. In the grassland habitat at site 1, only transects 2 and 3 were used. The seed stations directly under the trees (0m) were excluded to make a balanced design and ensure that I was only testing the open grassland habitat. All seed stations along a transect were combined to give the number "removed" and "left" for each combination of site, habitat, transect, exclosure, and seed species. In most cases this came to a total of 24 seeds for each data point. Some seed stations were removed from the analysis due to disturbance and other factors; if this was the case the total seeds for each data point was reduced accordingly.

Temporal change

To test for a change in predation patterns between years, the number of seeds removed over five days for *L. guineensi* and *P. peduncularis* was compared between the two years (trials 1 and 2). A mixed effects model with a binomial distribution was used. The numbers of seeds removed and left were combined into a response variable. Year, habitat, exclosure, and site, as well as the interactions of habitat, exclosure, and site with the year, were independent variables. As this showed a significant difference in predation patterns between the years it was not possible to compare data from the first trial to that of the second and third. As a result *N. buchananii,* and *P. viridiflorum* were excluded from the analyses and only data from the the two trials in the 2013/2014 season were used (trials 2 and 3).

Encounter rate

A seed station was classed as "encountered" if least one seed (of any species) had been removed. Seed stations were combined to give "encountered" and "not encountered" (out of a total of eight) for each combination of site, transect, habitat and exclosure type. A binomial mixed effects model was constructed with habitat, exclosure type, day (1 or 5), and their interactions as fixed variables, and trial (2 or 3), transect, and site as random variables. A second model was constructed using only the day 5 data to look for patterns in total encounter rate. Habitat and exclosure type were the independent variables while trial, line and site were random variables. The interaction between habitat and exclosure type was removed due to a non-significant term. Tukey tests were used to compare which subfactors within each of the fixed variables (ie control, invertebrate only and vertebrate only within exclosure type, and core, protected edge, unprotected edge, and grassland within habitat) were significantly different from each other.

Habitat, seed species, and predation guild effect

Only the data from the day 5 checks were used to analyse total removal levels. A mixed effects model with a binomial error distribution was used to allow for the inclusion of random effects. The number of seeds "removed" and "not removed" was combined into a single response variable. Fixed effects included habitat, seed species, and exclosure type, and their two-way interactions. Random effects included transect, site, and trial number to correct for pseudo-replication, and observation number corrected for over-dispersion (Elston et al., 2001). A type 3 Anova (car package) was used because it does not take into account the order in which factors are added into/taken out of the model, yet allows for interactive effects.

Microhabitat

A mixed effects model with a binomial error distribution was used to allow for the inclusion of random effects. The number of seeds "removed" and "not removed" was combined into a single response variable. Fixed effects included site, transect, habitat, seed species, and exclosure type, and the two-way interactions between site and habitat, seed species, and exclosure type. The random

effects were trial number to correct for pseudo-replication, and observation number to correct for over-dispersion.

Remnant tree

For the remnant tree analysis, transects at sites 1 and 3 were used. The first three lines (0m, 5m, 15m) at all three trees were used, but the last line (25m) was excluded as this line was only for the experiment involving a grassland habitat. Removal from the two seed stations of the same exclosure type at the same distance from each tree were combined. A seed station was classed as "encountered" if at least one seed (of any species) had been removed. Seed stations were combined to give "encountered" and "not encountered" for each combination of distance from the tree, site, transect, and exclosure type, which were then combined into a single response variable. A mixed effects model with a binomial error distribution was used to allow for the inclusion of random effects. Fixed effects included distance from tree, exclosure type, and their two-way interaction. Random effects included tree number, site, and trial number to correct for pseudo-replication, and observation number corrected for over-dispersion. A mixed effects model with a binomial error distribution was also used to investigate patterns in seed removal. "Removed" and "not removed" were combined into a single response variable. Fixed effects included distance from tree, seed species, and exclosure type, and the two-way interactions between distance and the other two variables. Random effects included tree number, site, and trial number to correct for pseudo-replication, and observation number corrected for over-dispersion.

Seed characteristics

To calculate seed characteristics of each species, 20 individuals of each species were randomly selected, measured and averaged. 'Hardness' is a three level factor where 1 = soft enough for a fingernail to mark, 2 = shell of seed brittle but crushable with fingernail, 3 = not able to be marked or damaged by fingernail. 'Colour' was treated as a four level factor – light, medium light, medium dark, dark. 'Dispersal method' can be vertebrate, wind, or ballistic. A mixed effects model with a binomial error distribution was used. "Removed" and "nor removed" were combined to create a response

variable. Fixed effects were weight, colour, hardness, dispersal method and exclosure type, and an interaction effect of each characteristic with exclosure type was included to allow for different predation guilds responding differently to different seed characteristics. Random effects included seed species, site, transect, and trial number to correct for pseudo-replication, and observation number corrected for over-dispersion.

3.3 Results

Temporal change

When *P. peduncularis* and *L. guineensis* are combined, 30 ± 3% of seeds were removed in the 2012/2013 trial and 23 ± 2% were removed in the 2013/2014 trial which is a significant difference ($p = 0.017$) (Table 3.2). There were also differences between the two years through interactions with other variables. The proportion of each species removed each year differed ($p<0.000$); removal of *L. guineensis* stayed relatively constant at 32% in 2012/2013 and 30% in 2013/2014, while removal of *P. peduncularis* was at 28% in 2012/2013 and dropped to 16% in 2013/2014 (Fig. 3.3). The pattern of removal among habitats differed between years ($p< 0.000$). Removal in the core and protected edge habitats stayed constant between the years (36% to 36%, and 22% to 20% respectively) while removal rates in the grassland (18% and 9%) and unprotected edge (34% and 27%) fell significantly between the first and second years (Fig. 3.4).

Table 3.2 Results from the binomial mixed effects model testing the effect of year, habitat, seed species and site, as well as their interactions, on the proportion of seeds removed from seed stations. Stars denote significance at $p = 0.05$.

Source of Variation	Chi Squared	D.F.	p value
Year	5.739	1	0.017 *
Seed Species	7.163	1	0.007 *
Habitat	3.729	3	0.292
Exclosure type	102.278	2	< 0.000 *
Site	1.652	1	0.199
Year * Seed Species	25.995	1	< 0.000 *
Year * Habitat	21.620	3	< 0.000 *
Year * Exclosure type	0.032	2	0.984
Year * Site	2.484	1	0.115

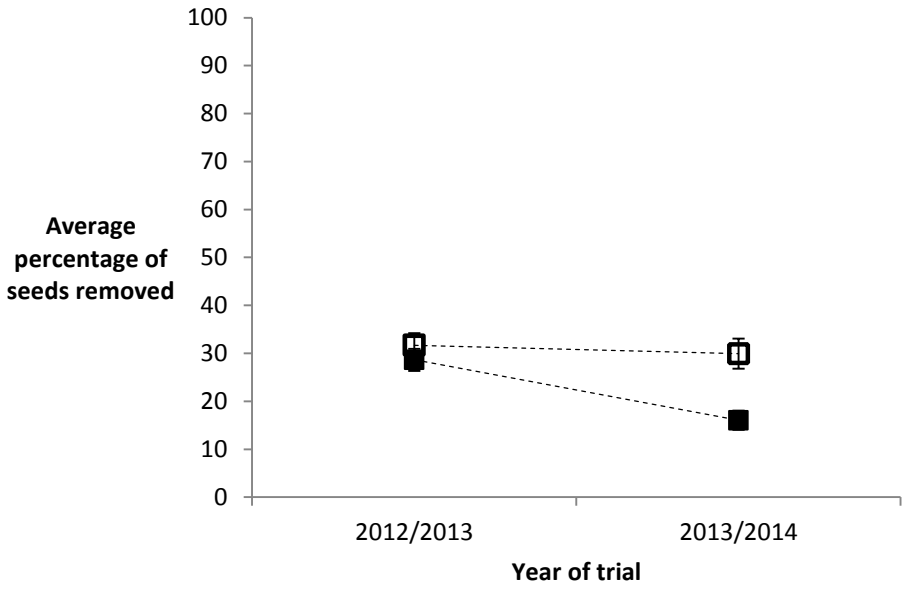


Figure 3.3 Average percentage of seeds removed of each species in each year ($p < 0.000$). Boxes = *P. peduncularis*, hollow boxes = *L. guineensis*. Dashed lines connect the same species between years. Error bars show ± 1SE, n = 48 for each point.

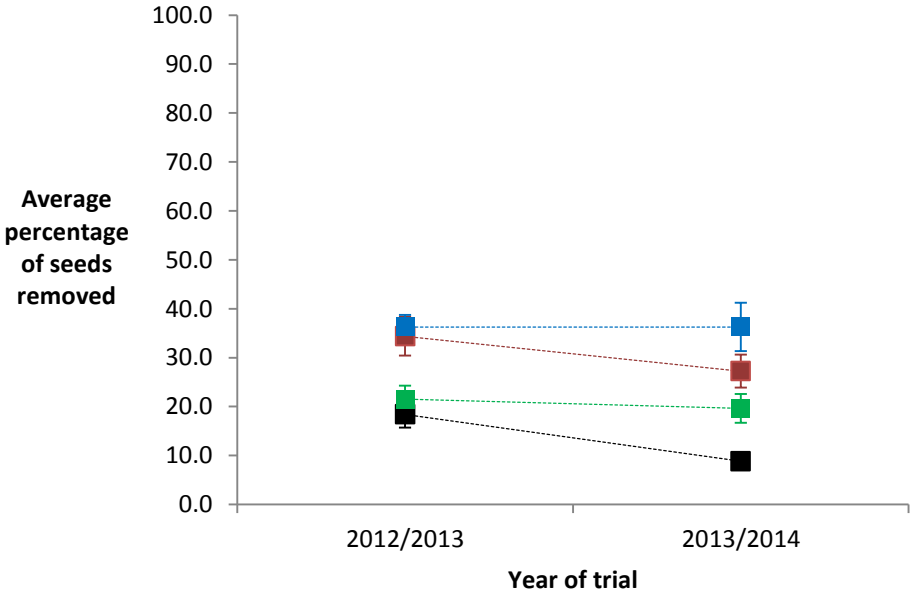


Figure 3.4 Percentage of seeds removed in each habitat by year ($p < 0.000$) . Black = grassland, red = unprotected edge, blue = core, green = protected edge. Dashed lines connect the same habitat type between years. Error bars show ± 1SE, n = 24 for each point.

Encounter rate

No significant interaction was found between observation day (1 or 5) and habitat ($p = 0.2190$, $df = 3$, $Chisq = 4.425$) or observation day and exclosure type ($p = 0.3427$, $df = 2$, $Chisq = 2.1417$). When only day 5 data was analysed, seed piles in the grassland habitat had a significantly lower probability of being encountered than seed piles in any of the other habitats ($p < 0.000$, $df = 3$, $Chisq = 33.43$) (Fig. 2.5). Seeds from in the vertebrate only piles were significantly less likely to be encountered than seed piles in other exclosure types ($p < 0.000$, $df = 2$, $Chisq = 23.06$) (Fig. 3.5). There was a small yet significant difference ($p = 0.0017$, $df = 1$, $Chisq = 9.83$) in the number of seed stations that were encountered in the two trials of the 2013/2014 season. In trial 2 (November/December 2013) 76% of seed piles were encountered over the five days, while 82% were encountered during the February/March 2014 trial.

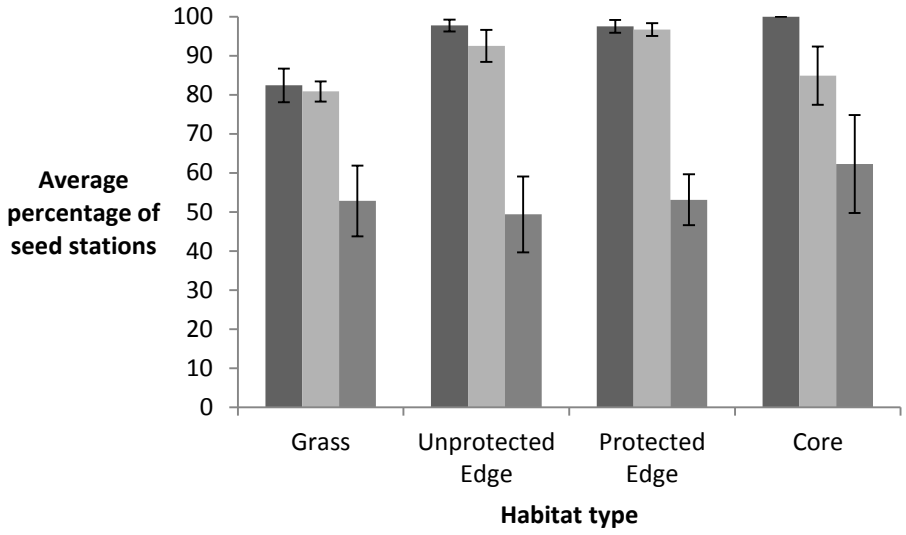


Figure 3.5 Average percentage of seed stations that had at least one seed removed during the five day trial, divided by habitat and exclosure type. Grassland habitats had significantly lower encounter rates than others ($p < 0.000$), as did vertebrate only exclosures ($p = 0.000$). Dark grey = control, light grey = invertebrate only, medium grey = vertebrate only. Error bars show ± 1SE, n = 8 for each bar.

Removal rate across habitat types, predation guilds and seed species

There is a significant difference in the removal rates of different seed species ($p < 0.000$) (Table 3.3). There was not a significant overall effect of habitat ($p = 0.092$) or exclosure type ($p = 0.063$) on total seed removal.

Table 3.3 Test statistics from binomial mixed effects model analysing the effect of each source of variation on removal rates of seeds. Stars denote positive values at $p = 0.05$.

Source of variation	Chi Squared	DF	P – value
Species	133.10	7	< 0.000 *
Habitat	6.45	3	0.092
Exclosure type	5.53	2	0.063
Species*Habitat	85.82	21	< 0.000 *
Species*Exclosure	111.13	14	< 0.000 *
Habitat*Exclosure	22.47	6	0.001 *

C. macrostachyus had the highest level of removal at 71 ± 5%, which was significantly higher than all other species tested, while *C. molle* had the lowest removal rate at 3 ± 1%, which was significantly lower than all other species (Fig. 3.6). The effect of seed species on removal rates is further examined in the "Seed characteristics effecting removal" section of the results.

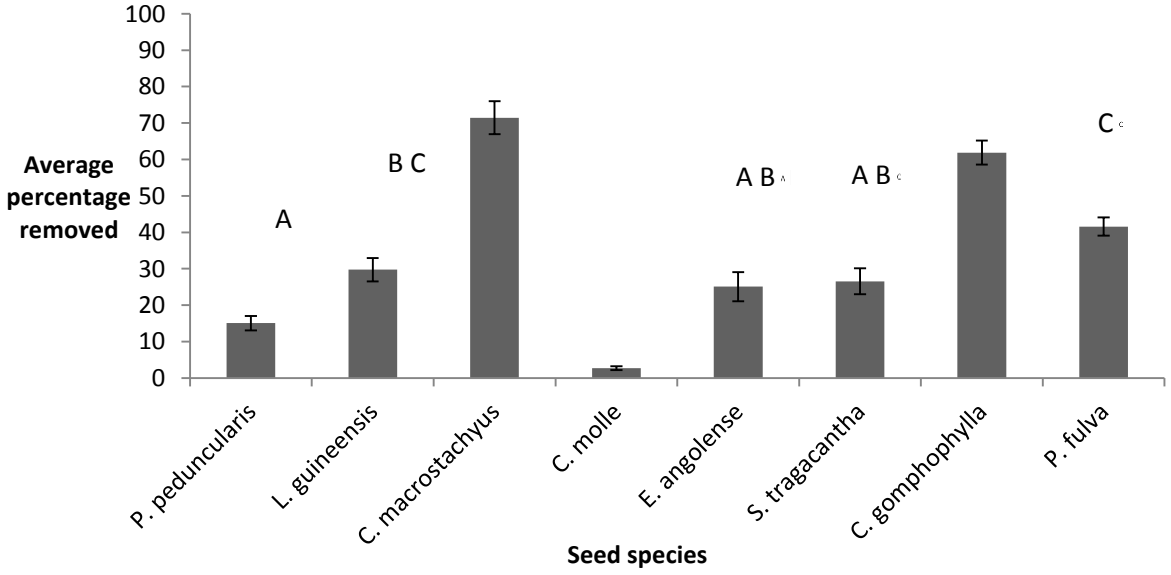


Figure 3.6 Average percentage of seeds removed for each of the ten seed species analysed (overall $p < 0.000$). Letters denote those pairwise combinations that are similar, all others are significant at $p = 0.05$. Error bars show ± 1SE, n = 48 for each species.

Although there seemed to be differences in the seed removal rates between habitat types this relationship is non-significant when the interaction effects between habitat and species and exclosure type are included in the model. Overall an average of 46 ± 3% of seeds were removed in core habitats and 26 ± 3% were removed in grassland (Fig. 3.7). There also seemed to be a pattern in the removal rates between exclosure types but as with the habitat differences this was non-significant. An average of 44 ± 3% of seeds were removed from control seed stations, 32 ± 3% from invertebrate only, and 27 ± 3% from vertebrate only (Fig. 3.8).

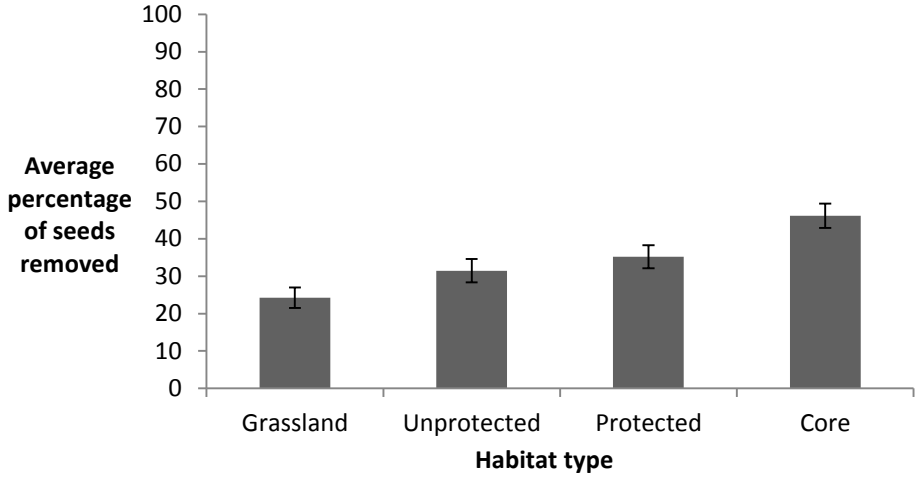


Figure 3.7 Average percentage of seed removal in each of the habitats (seed species and exclosure types combined). Differences are non-significant p = 0.092 . Error bars show ± 1SE, n = 96 for each habitat.

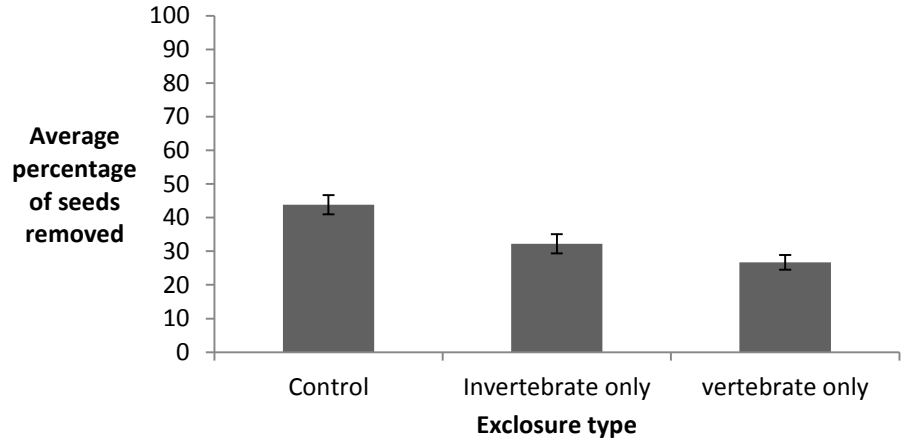


Figure 3.8 Average percentage of seed removal from seed stations of each exclosure type (seed species combined). Differences are non-significant p = 0.063. Error bars show ± 1SE, n = 128 for each exclosure type.

I found a significant interaction between habitat type and exclosure type (p = 0.001). Removal from the invertebrate only seed stations stayed relatively constant across all four habitats. In the core habitat removal from the vertebrate only seed stations was higher than in the grassland, unprotected edge, and protected edge habitats (Fig. 3.9). An overall significant interaction between habitat and seed species (p < 0.000) was driven by a few particular interactions: *C. macrostachyus* and *S. tragacantha* had significantly lower removal levels in grassland, *C. molle* significantly higher in unprotected edge, *L. guineensis* significantly lower in protected edge and grassland, and the most significant of all *E. angolense* significantly higher in the core (3.10). There is a significant interaction between exclosure and species (p< 0.000). The specific pairs that drive this interaction are the significantly lower removal of *C.macrostachyus* from vertebrate only stations, and the significantly lower removal of *E. angolense* and *S. tragacantha* from the invertebrate only stations (Fig. 3.11).

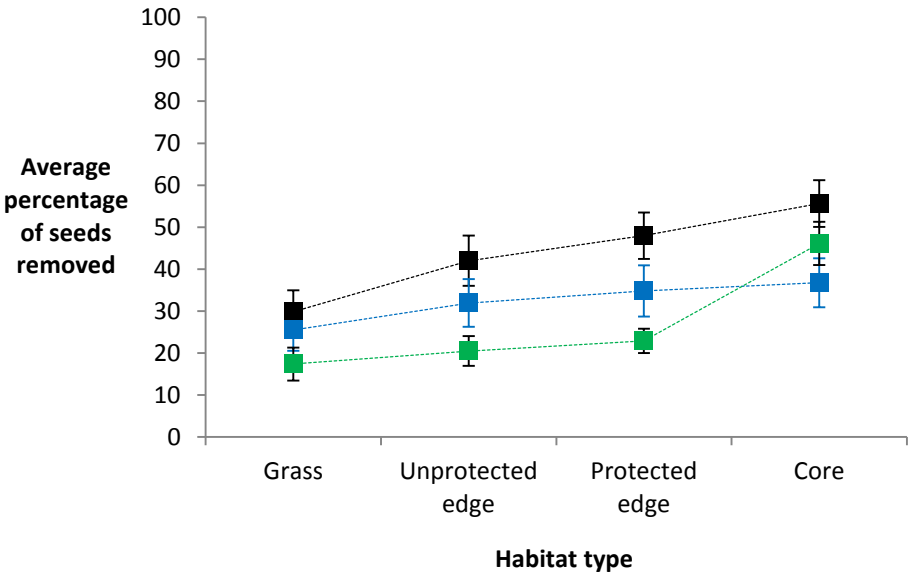


Figure 3.9 Average percentage of seeds removed for each combination of exclosure type and habitat type (interaction p = 0.001). Black = control, blue = invertebrate only, green = vertebrate only. Error bars show ± 1SE, n = 32 for each point. Dashed lines connect the same exclosure types between habitats.

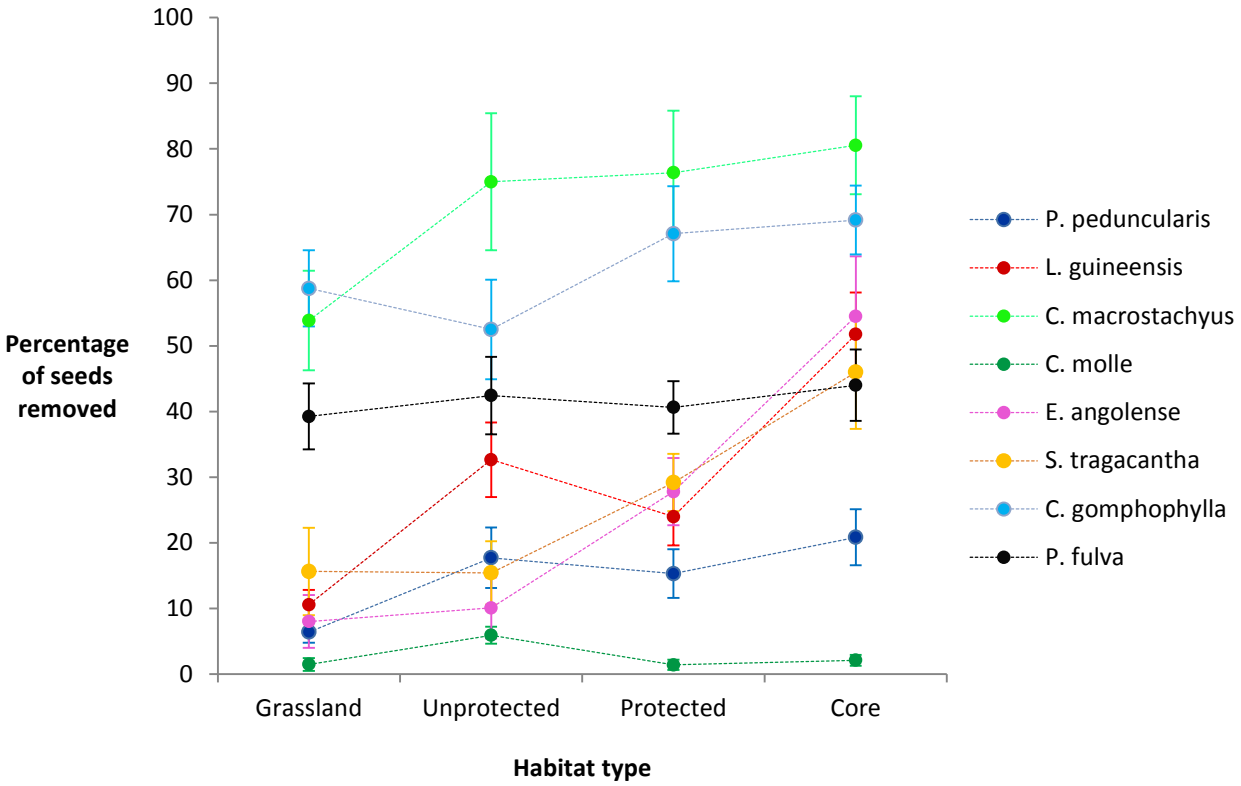


Figure 3.10 Average percentage of seeds removed for each combination of seed species and habitat type (interaction p< 0.000). Error bars show ± 1SE, n = 12 for each point. Dashed lines connect the same seed species between habitats.

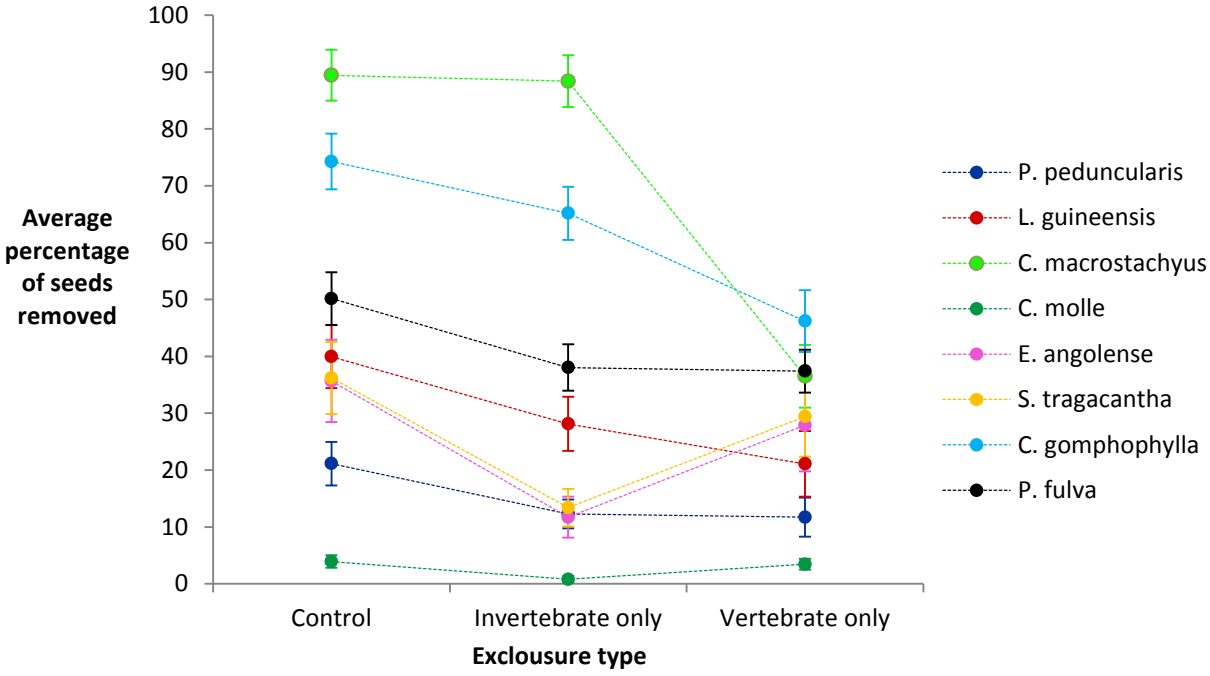


Figure 3.11 Average percentage of seeds removed for each combination of seed species and exclosure type (p < 0.000). Error bars show ± 1SE, n = 16 for each point. Dashed lines connect the same seed species between habitats.

Microhabitat

There is a small but significant difference in overall removal rates between site 1 which had 38 ± 2% of seeds removed, and site 2 which had 32 ± 2% of seeds removed (Table 3.4), but this was not a constant difference as a significant interaction between habitat and site was also found (Fig. 3.12). In both sites the core habitats had the highest removal, followed by protected edge, unprotected edge, and lastly the grassland habitat. Within habitats there were differences in removal rates between transects but due to high variation no significant pattern was found (Fig. 3.13). Small differences in removal of specific species between transects (particularly *E. angolense* in the Core) was observable, but not large enough to create a significant relationship.

Table 3.4 Test statistics from binomial mixed effects model analysing the effect of each source of variation on removal rates of seeds. Stars denote positive values at p = 0.05.

Source of Variation	Chi Squared	DF	P value
Site	22.08	1	< 0.000 *
Transect	3.60	1	0.058
Site*Species	4.74	7	0.691
Site*Exclosure	1.13	2	0.570
Site*Habitat	20.76	3	< 0.000 *

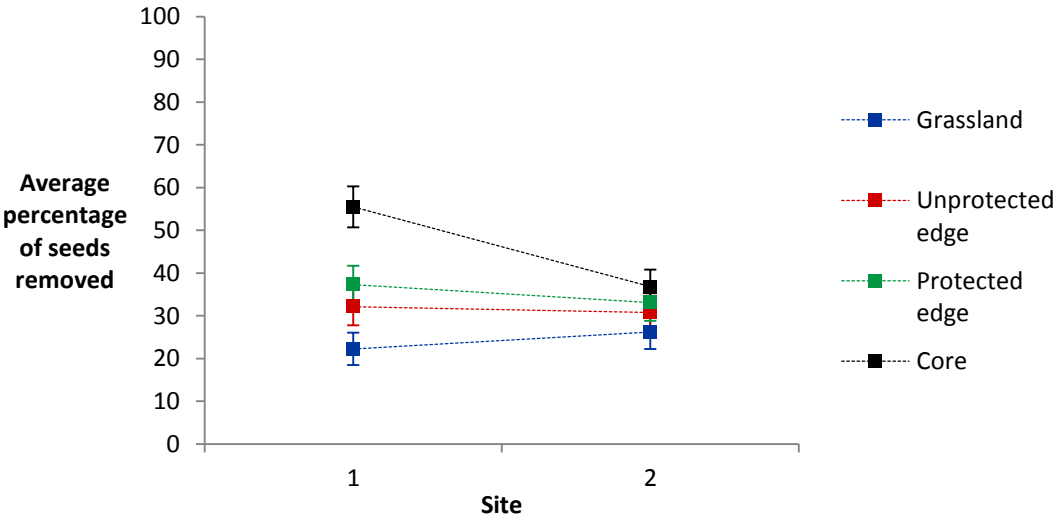


Figure 3.12 Average percentage of seeds removed for each combination of habitat type and site (p < 0.000). Error bars show ± 1SE, n = 48 for each point. Dashed lines connect the same habitat between sites.

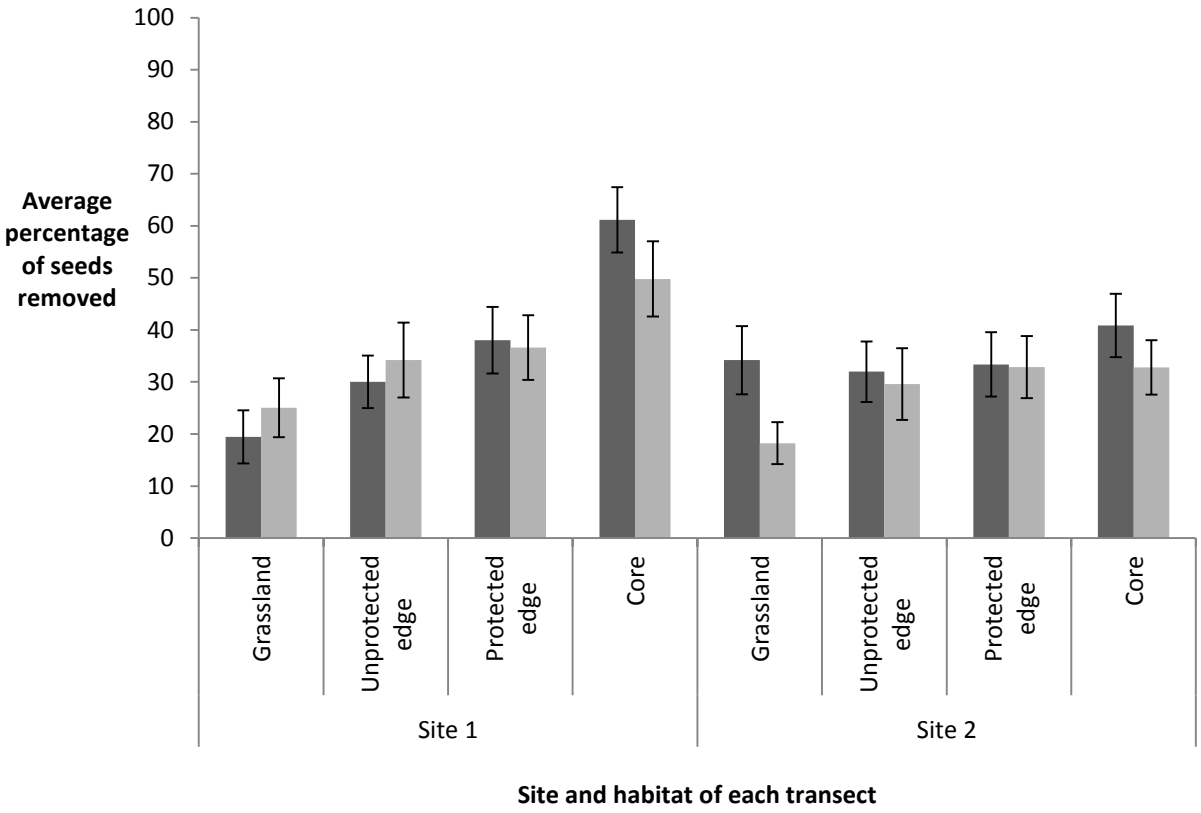


Figure 3.13 Average proportion of seeds removed in each of the eight microhabitat areas (four habitats repeated at two sites). The light and dark bars for each site/habitat combination represent the two different transects. Error bars show ± 1SE, n = 24 for each bar.

Seed characteristics

Despite restrictions on what seeds were available due to the season I managed to collect ten species in high enough numbers to be used, from a range of families and with different characteristics (see Appendix 6.8). Seed weights ranged from 0.0016g to 0.558g although most species were at the lighter end of this range with seven under 0.05g, one between 0.1g and 0.5g, and two over 0.5g. Seeds were a range of colours although for the purpose of statistical analysis they were divided into 'light', 'medium light', 'medium dark', and 'dark'. Two of the species - *Newtonia buchananii* and *Pittosporum viridiflorum*, were not included in removal analyses (see methods) so were also excluded here.

Seed hardness, colour, dispersal method and weight all had significant effects on removal rates (Table 3.5) There was a significant interaction between the weight of seeds and exclosure type ($p < 0.000$). The two heaviest seeds, *E. angolense* and *S. tragacantha* were predated less from invertebrate only stations than either the control or vertebrate only ones. In all the other species predation from invertebrate only was equal to or more than the vertebrate only stations (Fig. 3.14). The two darkest seeds used, *C. gomphophylla* and *C. macrostachyus* were also the two seeds with highest removal rates ($p = 0.030$, df= 1, Chisq = 4.71 at 71 ± % and 62 ± % removal respectively (Fig. 3.15). Seeds with ballistic dispersal (Fig 3.16), and those with a medium level of hardness (Fig. 3.17), also had the highest removal rates.

Table 3.5 Results from binomial mixed models analysing the relationships between seed characteristics and removal rates, and the relationship of these characteristics with predator guild (exclosure type). Stars denote significant values at $p = 0.05$.

Source of Variation	Chi Square	DF	P value
Weight	26.83	1	< 0.000 *
Dispersal	25.31	1	< 0.000 *
Hardness	67371	2	< 0.000 *
Colour	46.16	1	< 0.000 *
Weight*exclosure	20.73	2	< 0.000 *
Dispersal*exclosure	6.91	4	0.140
Hardness*exclosure	5.93	4	0.205
Colour*exclosure	4.79	2	0.091

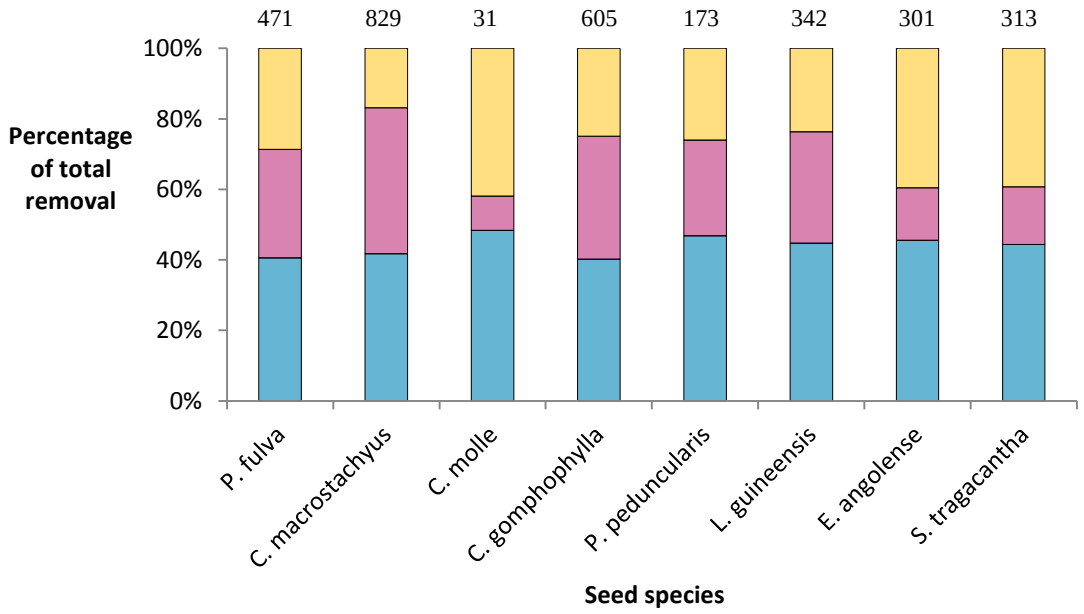


Figure 3.14 The seed removal from each of the exclosure types as a proportion of the total seed removal for each species (interaction $p < 0.000$). Total number of seeds for each species are included. Blue = control, pink = invertebrate only, yellow = vertebrate only. Seeds are arranged by weight from smallest (left) to largest (right).

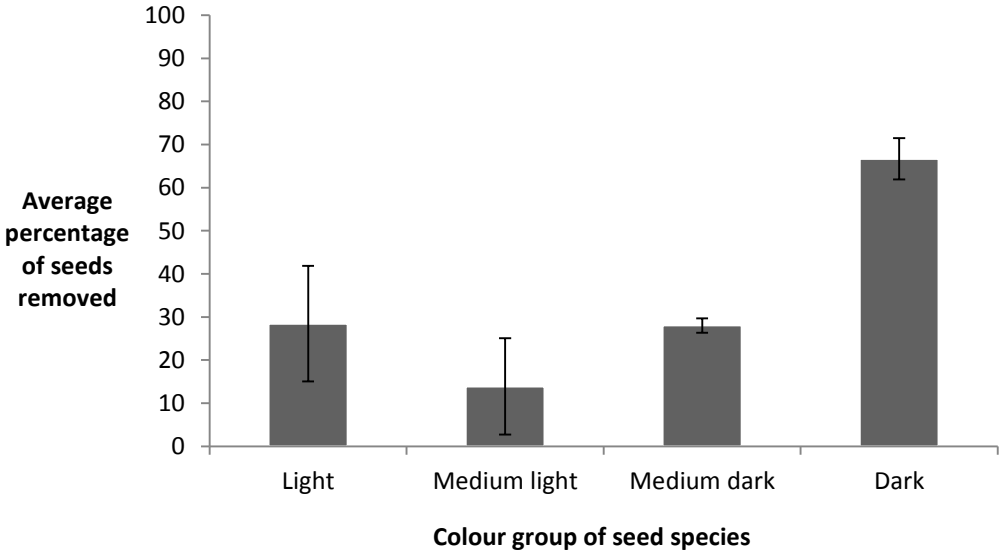


Figure 3.15 Average percentage of seed removal from species in each of the seed colour groups (effect of seed colour, $p < 0.000$) . Error bars are ± 1SE, n = 2 for each colour.

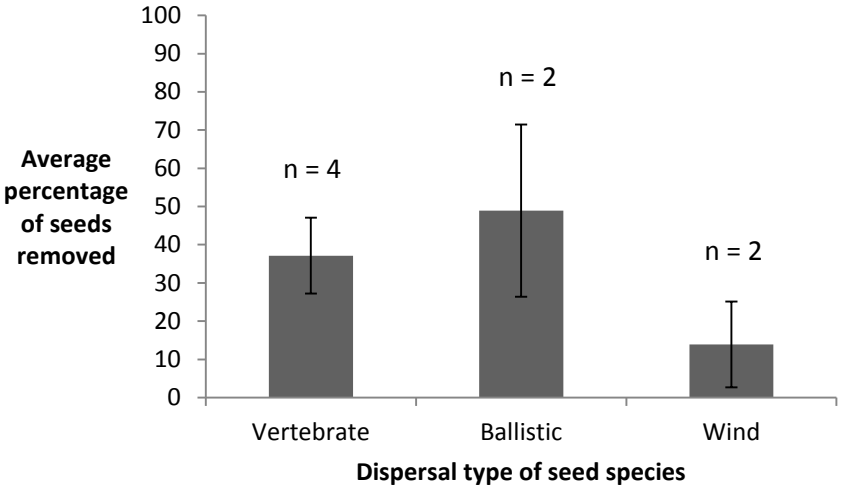


Figure 3.16 Average percentage of seed removal from species of each of the dispersal method groups (effect of dispersal method $p < 0.000$). Error bars are ± 1SE.

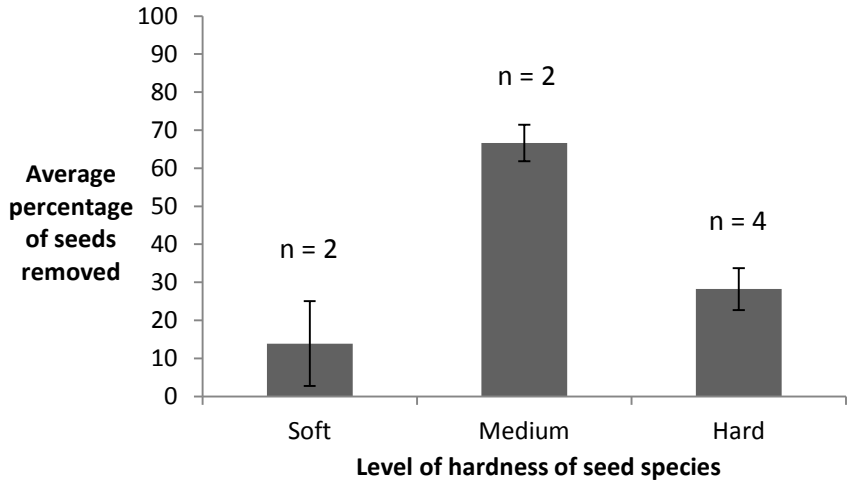


Figure 3.17 Average percentage of seed removal from species in each of the hardness levels (effect of hardness level $p < 0.000$). Error bars are ± 1SE.

Remnant tree effect

The distance away from the trunk of the tree had no effect on the encounter rate of seed stations ($p < 0.773$) (Table 3.6) (Fig. 3.18). Out of twelve possible seed stations (per tree, per distance, per trial) an average of 9.6 seed stations were encountered after five days for those directly under the canopy. On average, 8.9 seed stations were encountered at 5m, and 9.2 were encountered at 15m from the focal

tree. Encounter levels are significantly lower for vertebrate only seed stations than either control or invertebrate only ($p < 0.000$). Encounters rate of vertebrate only seed stations was significantly lower than both other exclosure types across all distances ($p < 0.000$).

Table 3.6 Test statistics from binomial mixed effects model analysing the effect of each source of variation on the encounter rate of seed stations. Stars denote positive values at $p = 0.05$.

Source of Variation	Chi Squared	DF	P value
Distance	0.08	1	0.773
Exclosure type	24.04	2	< 0.000 *
Distance*Exclosure type	0.97	2	0.616

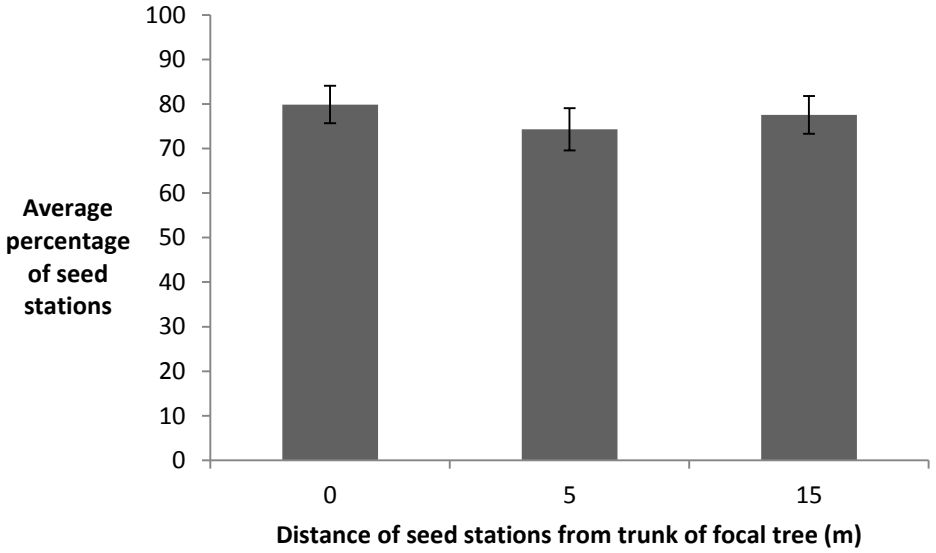


Figure 3.18 Average percentage of seed stations with at least one seed removed after the five day trial ('encountered' by a predator) at each distance from the remnant tree into degraded grassland ($p = 0.773$). Error bars show ± 1SE, n = 36 for each bar.

Total removal rates of seeds did not vary at different distances away from remnant trees (Table 3.7). An average of 28 ± 3% of seeds were removed from seed stations below the canopy, 22 ± 2% from those 5m away, and 27 ± 3% from 15m away from the focal tree, a non-significant difference ($p = 0.993$) (Fig. 3.19). Seed species and exclosure type both had individual effects on removal rates of

seeds ($p < 0.000$ for each) but neither interaction effect with distance was significant ($p = 0.201$, and $p = 0.734$ respectively).

Table 3.7 Test statistics from binomial mixed effects model analysing the effect of each source of variation on removal rate of seeds from seed stations. Stars denote positive values at $p = 0.05$.

Source of Variation	Chi Squared	DF	P value
Distance	0.00	1	0.993
Seed species	427.19	7	< 0.000 *
Exclosure type	27.90	2	< 0.000 *
Distance*Seed Species	9.64	7	0.201
Distance*exclosure type	0.62	2	0.734

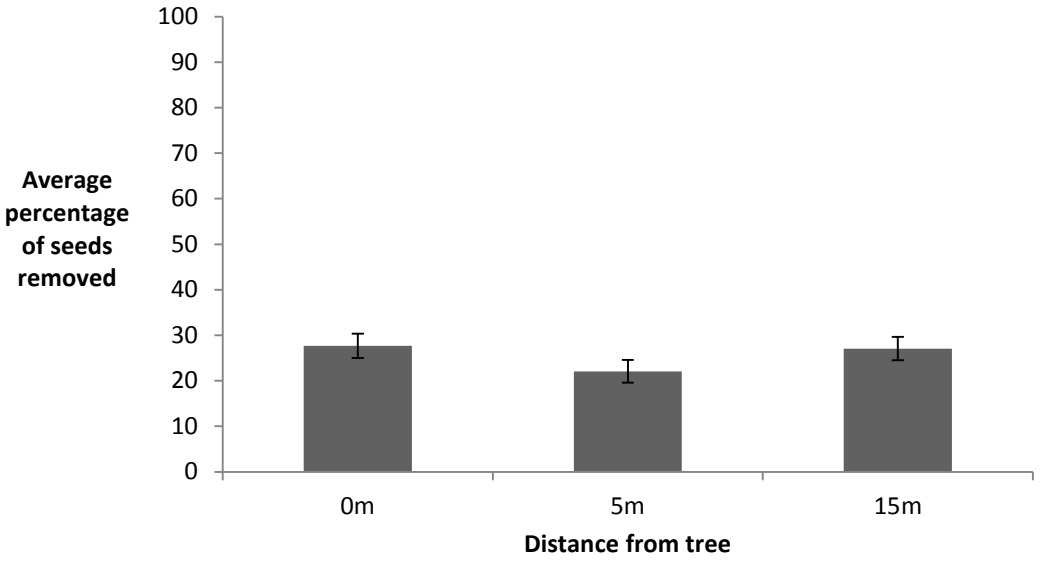


Figure 3.19 Average percentage of seeds removed from seed stations at increasing distances from a remnant tree into degraded grassland ($p = 0.993$). Error bars show ± 1SE, n = 144 for each bar.

3.4 Discussion

3.4.1 Factors influencing predation rates

Temporal variation

I found a significant difference in the overall predation rates of *L. guineensis* and *P. peduncularis* seeds between the two years. However as I only had two species to investigate this pattern it is difficult to state whether this is indicative of overall lower predation rates in the 2013/14 season, or if it is due to random fluctuations between the years. This result, along with the significant differences in removal rates between the two seed species and from different exclosure types, was consistent with other studies that found differences in removal rates between years (Willson & Whelan, 1990; Whelan et al., 1991; Shen et al., 2008). As a temporal variation in removal rate was not specifically examined in this experiment, not enough data was collected to make any predictions about these changes: whether they are following a pattern or if they are the result of a stochastic process. These findings did however further emphasise the need for large scale experiments over many years in order to fully understand predation rates in a system. Differences between seasons within a year have also been documented (Shen et al., 2008) but this was not examined in this study due to restricted field seasons.

Variation between habitat types within the reserve area

Habitat type had no significant effect on the overall level of seed removal in this experiment. However a pattern was observable where grassland had the lowest levels of predation, while the core habitats had the highest. Habitat effects on predation rates seem to be very system specific. Some other studies have found no relationship between habitat and removal rates (Holl & Lulow, 1997), in others core predation rates are higher than grassland ones (Hammond, 1995), while in some cases predation rates increase in disturbed habitats (Craig et al., 2011).

Effect of predation guild on removal rates

I found similar removal rates by both vertebrate and invertebrate predators. As ants are assumed to make up the majority of invertebrates that are removing seeds, this backs up previous studies that have suggested that ants play a major role as seed predators in tropical ecosystems (Nepstad et al., 1990; Kaspari, 1993). Encounter rates at invertebrate only stations were much higher than vertebrate only stations showing the high levels of area covered by invertebrate foragers. Although the level of encounter for vertebrate only seed stations was lower than those that ants had access to, total removal of seeds from these piles was similar. This limitation in vertebrates' ability to locate seed piles is probably due to their lower densities and the potential for their foraging patterns to leave gaps in the coverage of the environment. However since the total removal was similar between these exclosure types, more seeds must be removed from vertebrate only stations once they are located.

Interactive effects between predation guild and habitat differences in seed predation

The response of predators to habitat type is one of the factors that governs levels of seed removal in both this system and others (González-Rodríguez & Villar, 2012). Patterns of seed predation can be affected by the presence/absence of different guilds of predators and their differing foraging patterns (Christianini & Galetti, 2007; Mari et al., 2008). I found ants to be major seed removers throughout all habitats while predation by vertebrates was much lower across both the edge habitats and the grassland. In the core habitat vertebrate predation levels rose steeply to become comparable to that from ants. This could be due to active avoidance of areas with low canopy cover by rodents and other large vertebrates, thus concentrating their populations in the core forest, as has been found in other systems (Doust, 2011). Despite having comparable canopy cover to the core, edges do have different biological conditions that can affect the density and species composition of the animals using this habitat, resulting in different predation patterns (Vaaland Burkey, 1993; Murcia, 1995).

Habitat preferences of predators do not just operate at macrohabitat scales. I found significant differences in the overall level of predation between site 1 and site 2, and between the same habitat at these sites. Large variation was also observable between removal from the two transects within a

habitat, especially with vertebrate removal of the larger seeds in the core habitat at site 1. Other studies have found microhabitat differences in predation due to factors such as topography (Shen et al., 2008), and the density of leaf litter (Myster & Pickett, 1993). A stream runs near the transects in the core habitat of Site 1. As pouched rats may spend more time by streams during the dry season (pers. comm.) predator densities may be higher in these areas. These microhabitat differences can be corrected to a degree by having many test sites within a habitat, but it emphasises the need for large scale experiments to take these into account.

Predation rates of different seed species, and the effects of seed characteristics and predator guild

Significant differences in removal rates between seed species were found which is consistent with many other studies (Hulme, 1994). Most species have slightly lower removal in the vertebrate only seed stations which is consistent with a trend towards lower overall removal in that exclosure type. *C. macrostachyus* is the species with highest removal from control and invertebrate only stations and then drops in the vertebrate only exclosures allowing the extrapolation that, of the seeds tested, it was the most preferred species for ants. *C. macrostachyus* still has high removal compared to other species from the vertebrate only stations implying that it is still predated by vertebrates but not to the degree that it is by ants. *E. angolense* and *S. tragacantha* have low removal rates from the invertebrate only stations and higher from the vertebrate only and control stations suggesting that their primary predators are vertebrates.

Differential predation rates are often due to preferences of the foraging predator. Preference can be based on many traits such as seed size (Hulme, 1998a; Doust, 2011), nutritional content (Kelrick et al., 1986) and chemical/mechanical defences (García et al., 2005). Larger seeds tend to be preferred by larger animals such as rodents (Hulme, 1998a; Shen et al., 2008; Booman et al., 2009) and this trend was significant in my study with the two largest seeds, *E. angolense* and *S. tragacantha*, being removed much more by vertebrates than invertebrates. However their overall removal was quite low due to the more limited numbers of the larger vertebrates, a pattern that has also been found by Doust (2011) and Blate et al. (1998). Despite its small seed weight *C. molle* was primarily predated from

vertebrate only seed stations. As it is a wind dispersed seed the wings were left intact when the seeds were placed into the field. This increases the overall size of the seeds and possibly therefore makes them too large for ants to easily manipulate and move (eg.Rey et al., 2002). Hard seed coats have been found to limit seed predation, possibly due to the inability of many predators to open them (Blate et al., 1998; Doust, 2011). In this trial the seeds of a medium hardness were the most highly predated. This may be due to an interplay between the hardness and the size of seeds. The soft species that suffered only limited predation were the larger species (*C. molle*, *E. angolense*) which may have excluded them from ant predation. *C. macrostachyus* and *C. gomphophylla* are not as hard as *L. guineesis* and *P. fulva*, and yet are small enough for ants to remove. Significant effects of both the colour and dispersal method of the seeds were also found. Seed predation rates are often based on the nutritional content or palatability of the seed (Kelrick et al., 1986; Ohkawara & Higashi, 1994) but this was not investigated in this study.

Different seed species differed in the habitat in which they were most predated, a common pattern (Holl & Lulow, 1997; Bruun et al., 2010). *E. angolense* and *S. tragacantha* suffered higher predation in the core along with *L. guineensis*. All other species tested had relatively even removal rates across all habitats. This pattern is an indirect result of vertebrate predators preferring some seed species and specific habitats, for example predation of *E. angolense* is higher in the core, as vertebrate predation is more common in the core and they prefer *E. angolense*.

Seed predation below isolated trees in grassland

I found no significant differences in total predation or any interactions with predator species or seed species associated with remnant trees in grassland. This was unexpected considering the majority of studies show effects of these trees on predation, although some have found predation to be lowered by the trees (Holl & Lulow, 1997), while others have found an increase (Herrera & García, 2009). My results could be because the effect found in other studies is mainly due to habitat preferences of larger vertebrates, and yet predation from this guild is very limited in the grassland habitat. This may result

in any effect of the trees on this guild being too small for this experiment to detect, or it was masked by the higher total predation over all habitats from the invertebrate predators.

3.4.2 Limitations of this study and future directions

Pile size

Most seed predation studies show an increase in predation related to pile size (Willson & Whelan, 1990; Kaspari, 1993; Hulme, 1994). Many studies use large seed piles (e.g. 60 seeds per tray) which may artificially inflate predation rates by attracting predators to the area (Bruun et al., 2010). Density dependent preferences have also been recorded (Paine & Beck, 2007), where some seed species escape predation when they are in piles with other species – probably due to differences in palatability (García et al., 2007). I elected to use a small seed group size (eight seeds per pile) to try to simulate natural seed densities in the field.

An 'average' pile size is hard to establish due to seed densities in droppings being dependent on both the size of the seed and the disperser. The core environment also has much higher densities of natural seeds on the ground than the grassland areas, so the seeds in piles will be more unusual in the grassland habitat possibly leading to an increase in seed predation by attracting predators to the seeds (Bruun et al., 2010). However most seeds that naturally arrive in the grassland system are deposited in droppings so any increase in predation due to them being aggregated should still be within natural variation. I used piles of eight seeds regardless of the sizes of the individual seeds. By chance the seeds that were available for me to use in the third trial were larger than the seeds in the first two trials. This means that the absolute size of these piles was larger than the earlier trials, even though the seed number was the same, which may have artificially inflated the predation during this trial. In the future it would be interesting to study density dependent seed removal so we know both the effect of pile size for experimental design, but also how predators respond to seed densities in this system.

Removal does not equal predation

For this experiment I have used seed removal as a proxy for seed predation. However there is a growing body of literature showing that this is not always the case as rodents will often scatter-hoard larger seeds, while ants don't always predate removed seeds, instead leaving them in their nests to germinate (Jansen & Forget, 2001; Vander Wall et al., 2005; Cole, 2009). This means I may have reported levels of seed predation as higher than they actually are. I have tried to minimise this effect by mainly concentrating on smaller seeds (that don't get scatter-hoarded as much). It is not known what proportion of seeds removed by ants is consumed and how many are further dispersed. Seeds from species known to rely on ants for secondary dispersal were excluded from the trial. However other species in the *Croton* genus utilise ant dispersal although no specific information could be found for *C. macrostachyus*, so it remains a possibility that for this species in particular predation rates are not as high as my study shows. The experimental removal of anything suspected to function as an elaiosome, or ongoing studies about seed fate after removal, could help to answer whether or not seed removal for these species is an acceptable proxy for predation.

Limited seed species and seasonal differences

This study was carried out in the dry season as that is when I was available for fieldwork. However fruiting tree species are very limited during this time so I had very little choice about the seeds I used. This study would benefit from continuing it through a whole year and including many more seed species. This would give predation rates for more specific species but also permit more rigorous testing on the effect of seed characteristics on predation rates. The significant effect I found on predation rates by some seed characteristics may be a relic of the data set due to the relationship between the seed characteristics and the actual seed species. For instance *C. macrostachyus* and *C. gomphophylla* have the highest removal rates and are also similar sizes, the two darkest seeds, and the two seeds with medium hardness. This makes it difficult to truly represent which seed characteristics predators are basing foraging decisions on. A year-long study would also give us an idea of how predation rates vary across seasons.

3.5 Conclusions

Although there are limitations in this study due to the seeds and seed piles not being a totally natural state, I believe this still gives an accurate representation of the stochastic nature of seed predation rates in this system. Rates of seed removal were strongly dependent on the guild of the predator, the habitat that the seed is found in, and the species of the seed. All the patterns found are driven by the characteristics of the foraging predator and their preferences for certain seed characteristics and habitat types.

I found seed removal in grassland systems to be slightly lower than that in the core forest. I also found that remnant trees in these grassland areas did not increase seed removal rates under their canopies. Both these were unexpected results due to previous studies showing increase predation in both these habitats. However this is a very positive result for natural regeneration of forest seeds in grassland. Overall, each individual seed that is dispersed into the grassland has a greater chance of not being predated than those in the forest. Nonetheless this level of predation still has the potential to be a limiting factor. If seeds in these habitats are dispersal limited (i.e. more could grow in the grassland than are being dispersed there) then even this relatively low level of predation will further limit regeneration (Calviño-Cancela, 2007).

Differential predation rates between seed species can create a filtering process due to some species having higher survival rates than others. In the core forest it is hard to tell if increased rates of predation of some species will result in reduced seedling densities as it depends on the number of seeds produced by the tree, and the potential microsites for those seedlings. In the grassland the magnitude of a filtering process will depend on the seed rain coming in from the forest. For instance if the most preferred species is commonly dispersed then there is the likelihood that some seeds will escape predation and survive. However if a much preferred species is rare then high predation rates will have a greater effect of removing that species from the system.

Chapter 4: The Grass Sward

Impact on the Survival and Growth of Forest Seedlings

4.1 Introduction

4.1.1 Effects of the grass sward

When agricultural land is abandoned it frequently develops into a thick grass sward dominated by a small number of grass and herb species. This grass sward can modify a range of biotic and abiotic factors in these areas, thus slowing natural succession back to the original forest by creating an environment that is not favourable to the survival and growth of woody forest seedlings.

Some effects of the grass sward are direct; for example reducing radiation by physically shading the soil and seedlings (Ricard et al., 2003; Hoffmann & Haridasan, 2008), and/or competing for water and other soil nutrients (Benayas et al., 2005; Griscom et al., 2009). Other effects are through interactions with other parts of the system and are therefore less obvious. For example grass swards promote fire (Murphy & Bowman, 2012), and the use of the grassland by herbivores can be different to the forest thus changing the herbivory levels the seedlings are subject to (Dutra et al., 2011). The grass sward can have both positive and negative effects on woody seedlings and the net effect of grass depends on interactive effects between the grass itself, environmental conditions (Holmgren et al., 2000), the age and species of the woody seedlings (Hooper et al., 2002; Duncan & Chapman, 2003), and the limiting factors for seedlings in that area (Benayas et al., 2005). For example the grass sward competes with the seedlings for resources from the soil, a negative effect, but the effect of shading may have a positive effect by protecting the seedlings from radiation damage and lowering soil temperatures.

While most research has emphasised a negative effect the grass sward has on woody seedlings (Holl, 1998b; Rey Benayas et al., 2003; Gunaratne et al., 2011; Duclos et al., 2013), some studies have found the grass sward can instead facilitate seedling growth by buffering harsh environmental conditions (Pecot et al., 2007; Meli & Dirzo, 2013). Positive effects have been found by removing just the above-ground grass sward through mowing or cutting (Benayas et al., 2005) or by removing

root competition through trenching (Gerhardt, 1996). In other systems, for instance in the Neotropics, high survival of transplanted forest seedlings was found regardless of whether the grass sward was removed or not (Meli & Dirzo, 2013).

As a result of these interactive effects, the impact of the grass sward can be difficult to predict and very site specific. It is not always obvious in what systems and at what times it is advantageous to remove the grass sward and when it is best to leave it intact.

4.1.2 Aims of this trial

The purpose of this trial is to analyse the interactions between forest seedlings and the grass sward in the regenerating grassland around Ngel Nyaki forest, specifically looking at the effects of above and below ground competition. This will provide valuable information on the effect the grass sward is having on regeneration and direct decisions related to the management of the grass sward in order to promote natural regeneration and enhance the success of plantings.

Specifically this chapter addresses the following questions:

- Do above or below ground influences have the largest effect on seedling growth and survival?
- Does removing the grass sward promote or hinder seedling growth and survival?
- What biotic/abiotic factors does the grass sward affect that cause the observed effects on seedling growth and survival?

4.2 Methods

Study site

This study was carried out in and around Ngel Nyaki forest (see General Introduction for an in-depth discussion of this area). Five experimental replicates were set up in different fenced off grassland areas around the forest edge. Each replicate (site) was approximately 50m from the forest edge and a minimum of 200m apart (Fig. 4.1).

Figure 4.1 Map of forest showing location of each replicate. Adapted from Google Maps (2014).

Study species

Two seedling species were used: *Bridelia speciosa* (Phyllanthaceae) and *Psychotria succulenta* (Rubiaceae) *(*Fig. 4.2). These species were chosen as they are early colonising forest species, and also two of the most common species found self-seeding into the grassland. Seedlings were collected from the forest during the wet season (May/June) and raised in the nursery until August (second trial) or October (first trial) when 100 from each species were chosen to be planted into the field.

Figure 4.2 *Psychotria succulenta* (Left) and *Bridelia speciosa* (Right) seedlings.

1 month after planting, approximately 10cm tall.

4.2.1 Experimental design

This trial was carried out twice, over consecutive dry seasons (2012/13 and 2013/14).

At each site there were five treatments, each containing four seedlings of each of the two species (a total of 200 seedlings). Seedlings within a treatment were separated by 0.5m while treatments were separated by 1m. Five replicate sites were used, and the order of treatments was randomised in each.

Treatments

Experimental treatments were designed to differentiate between the above ground and below ground effects of the grass (Fig. 4.3). Above ground influences were removed by cutting the grass off at ground level. Above and below ground influences were removed by cutting the grass then cultivating the soil to remove the roots. Half the seedlings in each ground treatment were then artificially shaded

through the addition of wooden frames with grass roofs. A control treatment where seedlings were planted directly into the grass was also included.

Figure 4.3 Examples of treatments - a) Cultivated, b) Cut, c) Shade, d) Grass

Measurements

Soil moisture, and light levels were recorded to assess the effect of the grass sward on these abiotic factors. The method of collection of soil moisture data was changed between the two trials so only the data from 2013/14 was analysed. Soil in the top 20cm of soil in each treatment was measured fortnightly commencing one week before the end of the rainy season (end of October 2013) and extending into the middle of the dry season (end of February 2014). Measurements were taken with an Odyssey Data Logger by digging three separate holes 20cm deep within each patch to record moisture. Light levels for each treatment were taken periodically through the 2012/2013 dry season with an Odyssey Data Logger, at a height of 15cm above the ground. Three data points were recorded for each treatment at each time. A calibration was required for both the Odyssey data loggers. Unfortunately due to a corruption in the calibration file I was unable to calibrate the soil moisture meter. As the soil moisture was an important part of this study, and as it is a linear calibration that is required, I have included the analysis of the un-calibrated data to illustrate patterns in this data although I cannot calculate exact soil moisture levels. On December 24th 2013 I collected samples of soil from my plots and manually weighed and dried them to calculate percentage of water.

For the first trial, seedling height and survival were measured in October (at planting), January and April. For the second trial seedling height and survival recorded at planting (August), and every month from the end of October to the end of February. Survival was also recorded in April. Any observed damage to the seedlings (eaten by vertebrates, insect damage, fungus, drying) was recorded at the same time intervals to help explain differences in survival and growth rates between the treatments.

4.2.2 Statistical analysis

Analysis was carried out in R 3.0.3 (R Core Team, 2014) with the packages ‘car’ (Fox & Weisberg, 2011), ‘multcomp’ (Hothorn, Bretz & Westfall, 2008) and ‘lme4’ (Bates et al., 2014). Final p-values were calculated with either type 2 or type 3 Anova depending on the presence of significant

interactions. A p-value of < 0.05 was used as the significance level in all analyses. In each analysis, *a priori* linear contrasts were used to explore differences among treatments.

Seedling survival

Survival data from April both years was used to calculate survival rates. Site 3 from the 2012/2013 trial was excluded due to the site being destroyed by cattle midway through the trial. Binomial mixed effects models were constructed with treatment and species as fixed effects, and site and trial year as random effects. To look specifically at the effects of roots and shading on survival the control treatment was removed and treatments were re-described based on root presence/absence and shade presence/absence. A mixed effects model was then run with root (as a factor), shade (as a factor), and their interaction term as fixed effects, and site and trial as random effects.

Total Growth

Only data from the 2013/2014 trial was used for this analysis as heights at the end of the dry season were not recorded in trial 2. For trial 2 the February height data was used as the final height. Growth was calculated as the percentage increase from start height. A mixed effects model with treatment and species as fixed effects and start height and site as random effects was constructed. To look specifically at the effects of roots and shading on growth the control treatment was removed and treatments were re-described based on root presence/absence and shade presence/absence. A mixed effects model was then run with root (as a factor), shade (as a factor) and their interaction term as fixed effects, and site as a random effect.

Effect of start height

The effect of seedling start height was analysed using linear models with percentage growth and absolute end height as separate dependent variables, and start height, species and treatment as fixed effects.

Light and moisture levels

Both light levels and moisture levels were analysed with linear mixed models with time and treatment as fixed variables, and site as a random variable. Only moisture measurements from the second trial were analysed due to a change in data collection methods between the two trials. Two linear models were used to check for a relationship between the soil moisture levels in February, and the percentage height increase and survival rates of seedlings in plots.

Seedling damage

Incidence of different types of plant damage was analysed as a series of individual regressions with the levels of each type of damage dependent on treatment.

4.3 Results

Survival

The treatment that the seedlings were planted into had a significant effect on their survival rate ($p < 0.000$, Table 4.1). The cut & shade and cultivated & shade treatments had highest survival rates and were significantly different to all other treatments (Fig. 4.4). The control treatment had the lowest survival both years although it was not significantly different to the cut treatment overall. There was no significant difference in survival rates between the two species used in this experiment ($p = 0.947$). The interaction effect was also non-significant showing no difference in species responses to treatments. Survival differed significantly between the two years ($p < 0.000$) with 47.5 ± 14 % of seedlings surviving through the study period in 2012/2013 and 67 ± 11 % surviving in 2013/2014.

Table 4.1 Results from two different mixed effects models analysing the effect of each of the sources of variation on the survival of seedlings. Stars denote significance at $p = 0.05$.

Source of Variation	Chi Square	DF	P
Treatment	75.805	4	< 0.000 *
Species	0.004	1	0.947
Treatment*Species	7.612	4	0.107
Year	22.257	1	< 0.000 *
Shade (present/absent)	42.75	1	< 0.000 *
Roots (present/absent)	1.89	1	0.049 *
Shade * Roots	1.32	1	0.254

Both the removal of roots and the addition of shade increased seedling survival in both years ($p= 0.049$ and $p < 0.000$ respectively) (Table 4.1). The effect of shade application is larger with final survival rates 72% when roots were removed, 62% with roots present, 85% with the addition of shade, and 48% without shade. Although there seems to be a pattern in the interaction between root removal and the application of shade (Fig. 4.5) this is non-significant ($p = 0.254$). There were no significant interactions between the year of the trial and any effects of shade application and root removal (Table 4.2).

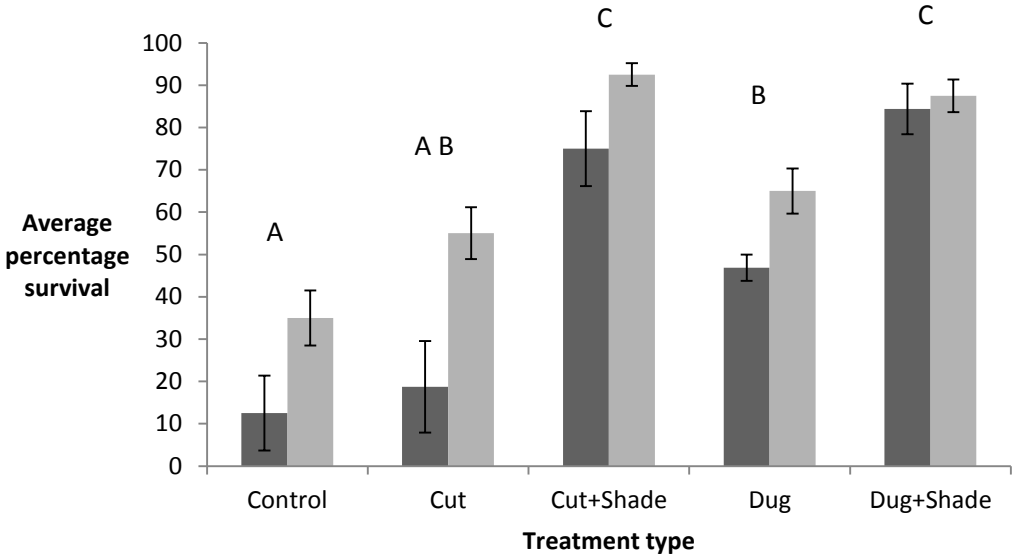


Figure 4.4 Average percentage of seedlings that survived the period between October and April in each treatment type. Dark boxes = 2012/2013 trial, light boxes = 2013/2014 trial. Letters denote similar pairwise combinations between treatments (years combined) at p = 0.05.

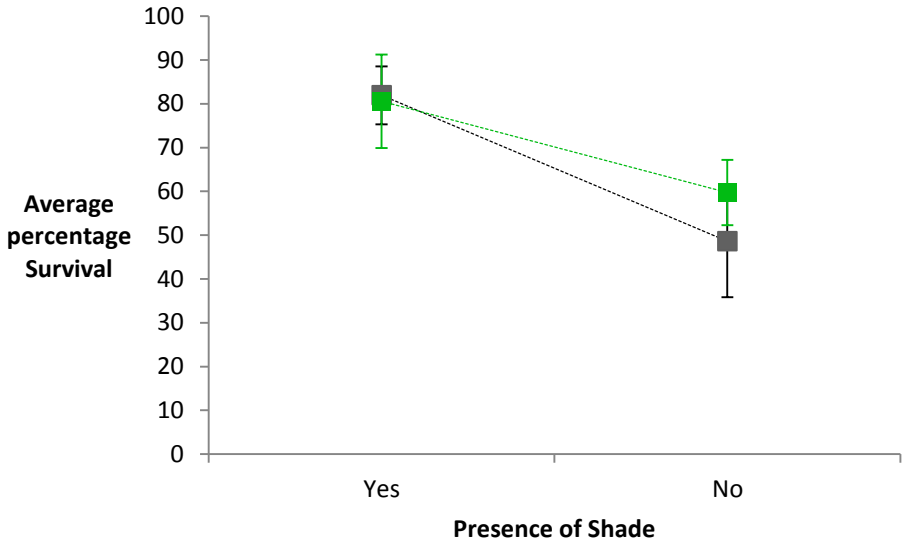


Figure 4.5 Average survival of seedlings planted in differing root/shade treatments (interaction p = 0.254). Black = roots present, green = roots removed. Error bars are ± 1SE.

Growth

Total percentage growth over the dry season was dependent on the treatment that the seedling was planted into ($p < 0.000$) (Table 4.2). Cut & shade and cultivated & shade treatments promoted significantly faster growth rates than the other three treatments (Fig. 4.6). *P. succulenta* (87 ± 11% increase over five months) had a significantly higher growth rate than *B. speciosa* (68 ± 9% increase over five months) ($p = 0.001$). The application of artificial shade significantly increased the growth rates of seedlings ($p < 0.000$), while the removal of roots had no impact ($p = 0.981$) (Fig. 4.7).

Table 4.2 Results from two different mixed effects models analysing the effect of each of the sources of variation on the percentage height increase of seedlings. Stars denote significance at $p = 0.05$.

Source of Variation	**Chi Square**	**DF**	**P**
Treatment	40.48	4	< 0.000 *
Species	10.29	1	0.001 *
Treatment*Species			
Shade (present/absent)	35.34	1	< 0.000 *
Roots (present/absent)	0.00	1	0.981
Shade * Roots	0.38	1	0.537

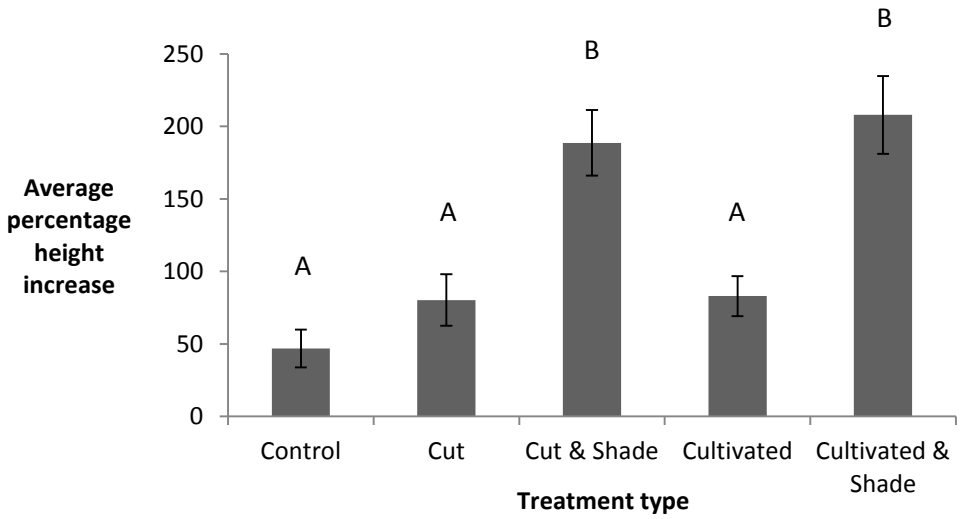


Figure 4.6 Graph showing average percentage height increase between October 2013 and February 2014 of surviving seedlings in each of the five treatments. Letters denote non-significant pairwise differences at $p = 0.05$. Error bars are ± 1SE.

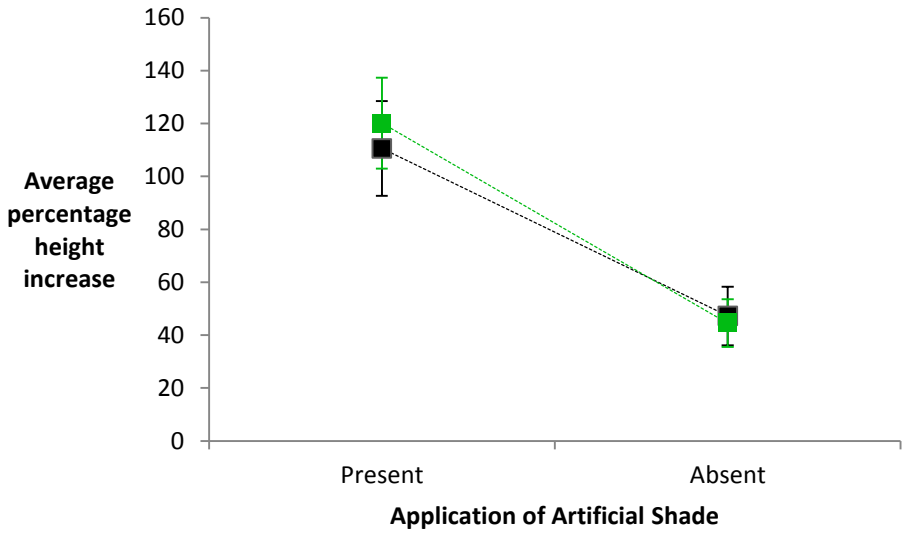


Figure 4.7 Average percentage height increase of seedlings planted in differing root/shade treatments (interaction p = 0.254). Black = roots present, green = roots removed. Error bars are ± 1SE.

Start height

Seedlings were planted randomly into treatments so start heights were constant (F = 0.2922, df = 4, p = 0.8828). The percentage increase in height is dependent on the original height of the seedling (p < 0.000, df = 1, ChiSq = 81.22). Part of this is due to the *P. succulenta* being smaller on average than the *B. speciosa* at planting, but even when the species is included as a factor, the start height is still significant as the pattern is consistent within each species (Fig 4.8).

The absolute final height of seedlings is not significantly related to their start height (p = 0.454, df = 1, ChiSq = 0.5605) (Fig. 4.9). Through having a higher growth rate the shorter seedlings caught up to the taller seedlings. Absolute height of seedlings at the end of the trial is dependent on treatment (p = 6.762e-11, df = 4, ChiSq = 53.4798) and species. *B. speciosa* are significantly taller at the end of the trial than *P. succulenta* (p = 4.983e-05, df = 1, ChiSq = 16.4547).

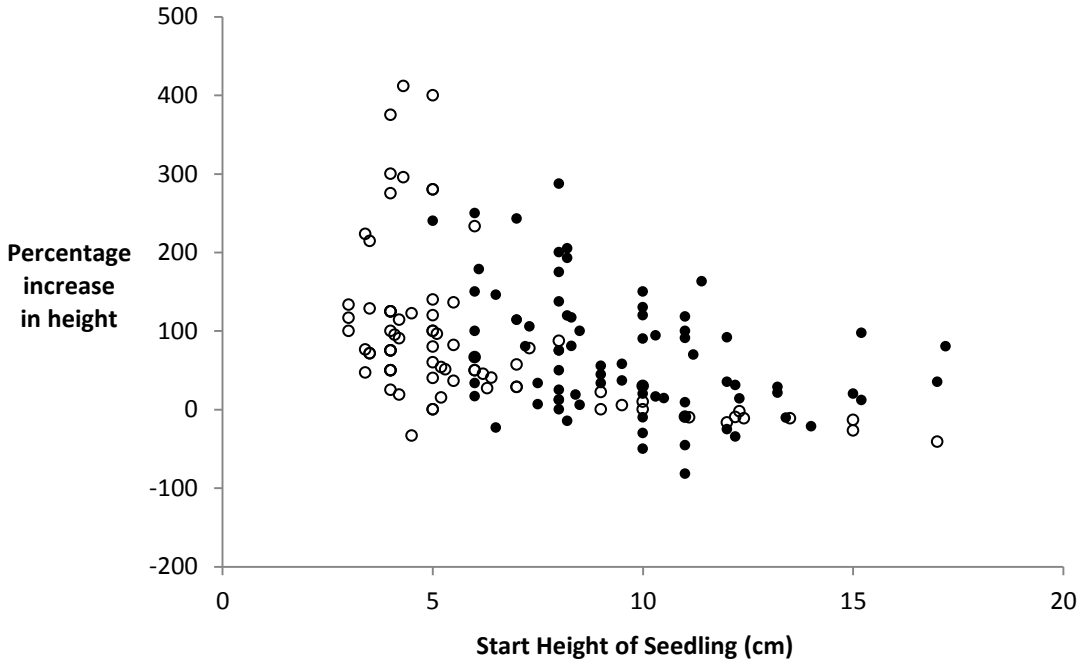


Figure 4.8 Total increase in height (as a percentage of start height) in relation to the start height ($p < 0.000$). Hollow dots = *P. succulenta*, Black dots = *B. speciosa*.

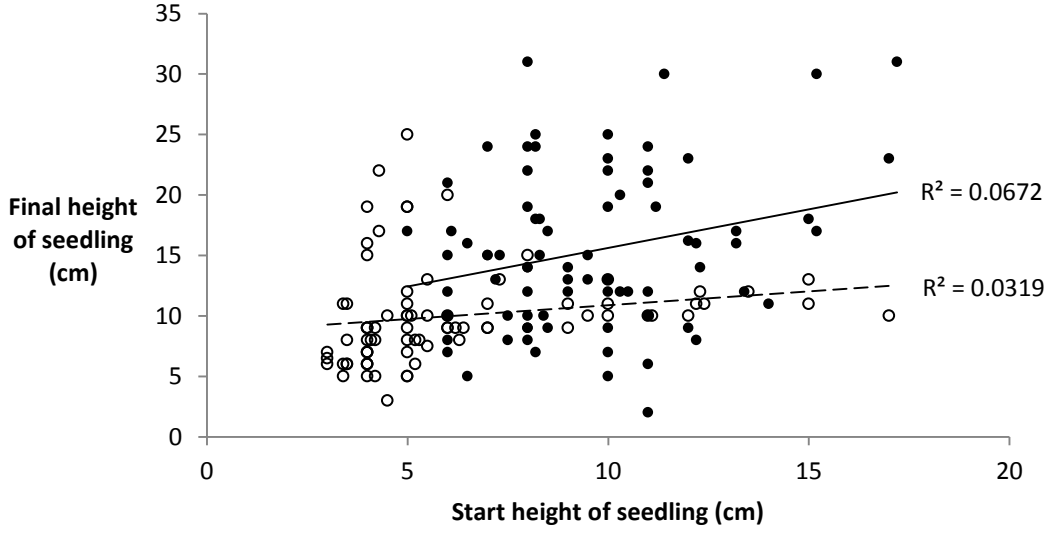


Figure 4.9 Relationship between start height and final height of seedlings ($p = 0.454$). Black dots and solid trendline = *B. speciosa*, Open dots and dashed line = *P. succulenta*.

Plant damage

Insect herbivory did not differ significantly in incidence between the five treatments (p = 0.751) (Table 4.3). Levels of vertebrate herbivory differed between treatments (p = 0.002) with the herbivory in the cut treatment significantly higher than that in the control and cut & shade treatments (Fig. 4.10). Leaf desiccation was significantly different between habitats (p = 0.001). The cultivated & shade treatment had least plants showing signs of drying and was significantly lower than the cut, cultivated, or control treatments (Fig. 4.11).

Table 4.3 Results of three separate Anova's between the incidence of plant damage and each treatment type. Stars denote significance at p = 0.05.

Source of Damage	Chi-Square	DF	P value
Vertebrate herbivory	17.17	4	0.002 *
Invertebrate herbivory	1.97	4	0.751
Desiccation	19.63	4	0.001 *

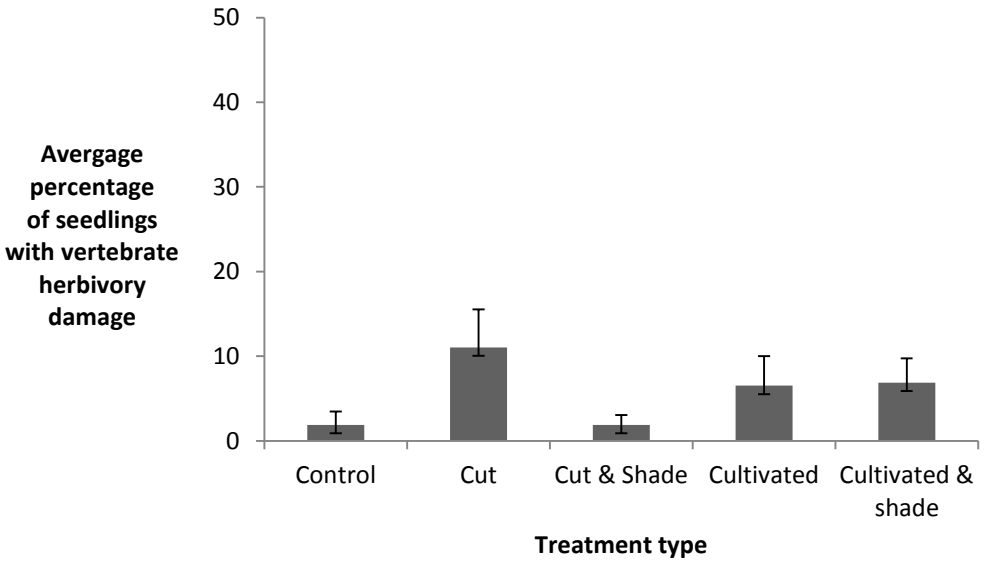


Figure 4.10 Average percentage of seedlings damaged by vertebrate predation in each of the treatments over the trial period (p = 0.002). Error bars are ± 1SE.

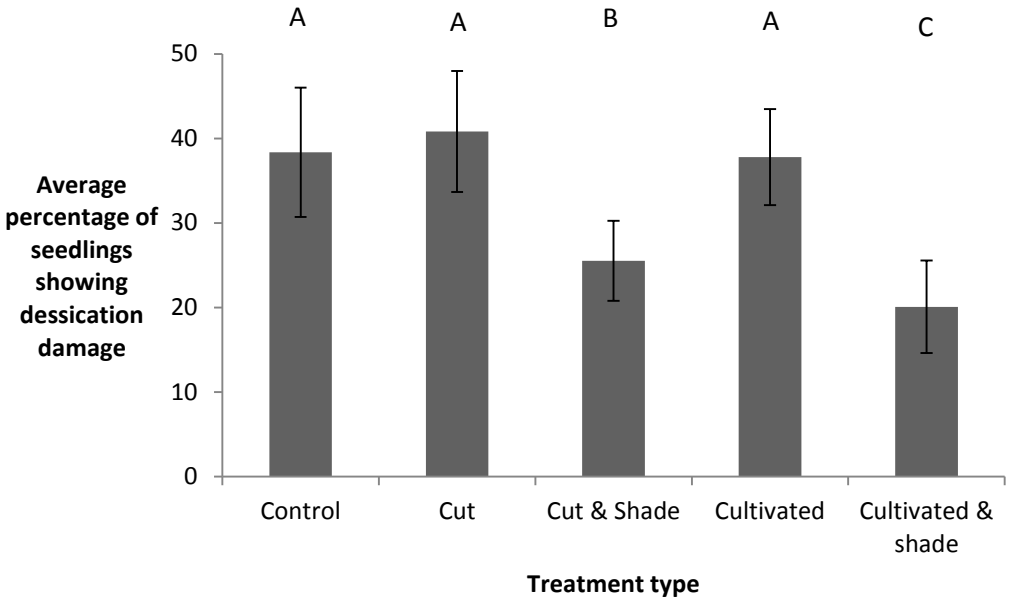


Figure 4.11 Effect of treatment type on the average number of seedlings in each subplot to have desiccation damage (p = 0.001). Letters denote non-significant pairwise comparisons.

Light levels

Treatment, month, and their interaction term all have significant effects on levels of light getting to the seedlings (Table 4.4). The removal of the grass through cutting significantly increased light levels while the application of artificial shade reduced that again and mimicked the light levels in the grassland (Fig. 4.12). Light levels decreased over all treatments as the dry season progressed, probably due to the increase in cloud cover, but this was most noticeable in the cut and cultivated treatments where the seedlings and the meter were directly exposed to the sun.

Table 4.4 Results from linear mixed model analysing the effect of each of the sources of variation on the light levels in each subplot. Stars denote significant factors are p = 0.05.

Source of Variation	Chi-Square	DF	p value
Treatment	263.94	4	< 0.000 *
Time	24.84	1	< 0.000 *
Treatment * Time	25.60	4	< 0.000 *

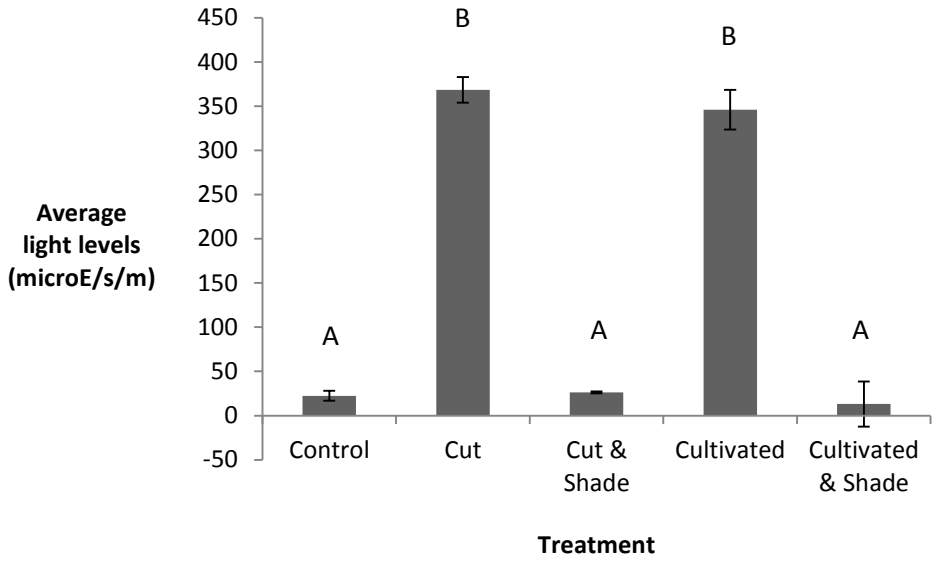


Figure 4.12 Average light levels (microE/s/m) in each of the five treatment types ($p < 0.000$). Letters show which pairwise combinations are non-significantly different at $p = 0.05$. Error bars show ± 1SE, n = 12 for each bar.

Moisture Levels

The results in this section have all been calculated with un-calibrated data (see methods section for explanation). The level of soil moisture is significantly related to both the treatment and the month the measurement was taken ($p = 0.004$ and $p = 0.012$ respectively) (Table 4.5). The cut & shade treatment has significantly higher soil moisture than the grass treatment, while in all treatments the soil gets dryer as the dry season progresses (Fig. 4.13).

A significant relationship between moisture levels and seedling survival was found despite hight levels of variation ($p = 0.007$, df = 1, ChiSq = 7.19) (Fig. 4.14), however there was no relationship between moisture levels and the relative height increase of seedlings ($p = 0.108$, $F = 2.86$). The soil samples collected from the cut & shade and cultivated & shade treatments in December 2013 were 36 ±1% water by weight.

Table 4.5 Results from the linear mixed model analysing the effect of treatment and month on soil moisture levels. Stars denote a significant effect at p = 0.05.

Source of Variation	Chi-Square	DF	p value
Treatment	15.12	4	0.004 *
Month	6.35	1	0.012 **
Treatment * Month	1.56	4	0.816

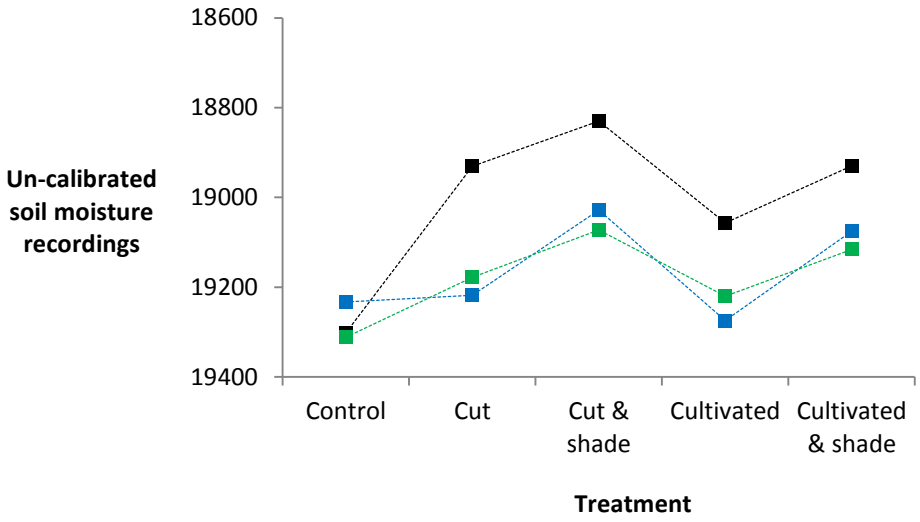


Figure 4.13 Relationship between treatment type and month measured with soil moisture levels. Y axis is inverted as it is uncalibrated data and smaller numbers = higher water levels while larger numbers = lower soil moisture levels. Black = October, blue = November, Green = December.

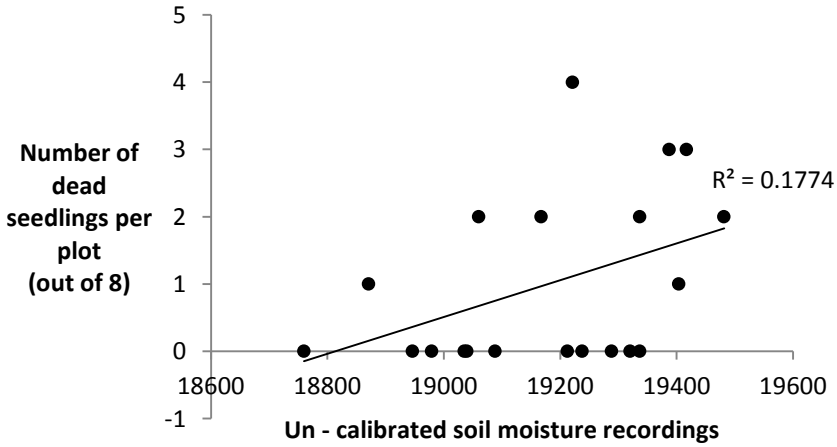


Figure 4.14 Relationship between the level of soil moisture and the death rate of seedlings (p = 0.007). X-axis gives un-calibrated soil moisture readings, smaller numbers = higher water levels, larger numbers = lower soil moisture levels.

4.4 Discussion

4.4.1 Effects of the grass sward

Effect of shade

Of the treatments tested, the two that most increased seedling survival and growth were the cut & shade and cultivated & shade treatments, which coincided with the strong positive effect of artificial shading on both these seedling measures. This positive effect of artificial shading was not a surprise as it has been recorded in many other tropical systems (Holl, 1998b; Ricard et al., 2003; Benayas et al., 2005). However the apparent reason for this pattern is less intuitive. Shading both decreased light at ground level and was associated with increased moisture levels in the soil. The natural shade of the control treatment produced similar light levels as the artificial shade, but was associated with lower soil moisture levels. The control treatment also had much lower seedling survival and growth than the two artificially shaded treatments. This implies that the observed effect of artificial shading is not due to protection from sun damage, but instead through shading the ground and maintaining higher soil moisture levels (Benayas, 1998; Thaxton et al., 2012).

Effect of roots

Root removal had no significant impact on the growth of seedlings but did have an effect on survival rates, although the magnitude of this effect is smaller in all analyses than the effect of shading. The likelihood of seedlings to be showing visual signs of desiccation damage was also significantly different between the cultivated & shade and the cut & shade treatments. Many other studies have also found a negative effect of roots where digging a trench around seedlings, thus removing competing roots, has resulted in an increase in survival and growth of seedlings transplanted into regenerating areas (Gerhardt, 1996; Gunaratne et al., 2011). Although not a significant interaction it appears that the positive effect of root removal is more pronounced when there is no artificial shade.

In these harsher environments, where the soil moisture is already lower due to the lack of shading, the smaller effect of the root competition seems to make a larger difference.

Effect of cutting grass at ground level

Unfortunately, due to not having a plot of grass that was covered by artificial shade, I have no specific data on the effect of leaving an intact grass sward under artificial shade. However I am able to draw some conclusions about the effect of the above ground grass sward through comparisons with the other treatments. Many experiments have shown that the cutting of the grass at ground level (without root removal) increases seedling survival and growth (Benayas et al., 2005; Thaxton et al., 2012; Duclos et al., 2013), even when combined with artificial shading (Thaxton et al., 2012).

The low survival and growth in the control (grass) treatment was unexpected. I had expected the control treatment to be similar to the cut & shade treatment, considering the leaves of the grass and the artificial shade resulted in similar light levels on the ground. The fact that these treatments produced such different results implies there were other factors influencing seedling survival in the control that I did not measure, such as disease incidence or competition for nutrients. The cut and cultivated treatments have similar soil moisture levels, seedling growth, and seedling survival levels, and all of these are higher than that of the control treatment. Competition for water from the grass sward is a common limiting factor for forest seedlings (Rey Benayas et al., 2003; Thaxton et al., 2012), but this result suggests that cutting the grass off at ground level does cause a reduction in this competition even though the roots are still intact.

I observed that over the period of the experiment the grass sward in the surrounding areas dried and thinned, presumably as a response to increasing dryness in the system. As the artificial shading increased the growth of the seedlings, there is a high chance that it may have a similar effect on the grass sward. As I did not shade any grass plots this is unable to be verified, but it was found in a similar experiment by Benayas (2005) where the shade increased the height of the weeds as well as

the seedlings. If this effect does occur in this system as well, then that would be another reason cutting the grass before shading would be recommended.

Vertebrate predation was significantly higher in the cut treatments, possibly due to the removal of the grass making the seedlings more obvious. The frames holding the artificial shade may also protect seedlings from large vertebrates, although this does not explain why herbivory in cultivated treatments was lower. Smaller herbivores such as grasscutter rats and rabbits could still access seedlings under the shade cover, and these animals were found across all sites, helping to explain why herbivory in the cultivated & shade treatment was also raised.

4.4.2 Limitations of this trial and future directions

Care needs to be taken when extrapolating these results to other species that might be planted into these grasslands. Both species used in this trial are early successional trees, but seedlings from species of different successional stages are likely to have different responses to vegetation removal (Duncan & Chapman, 2003). Late successional seedlings tend to be more adapted to shaded environments so may gain larger benefits from lower light levels under the shade and grass. The age of the planted trees can also impact on their response (Duncan & Chapman, 2003) and as all the seedlings used in this trial were under one year old no inferences can be made about the effect of vegetation removal on saplings. If it is possible to source enough seedlings to run a similar trial with more, different species, of different successional stages this would allow us to see the effect of the grass sward on these other species. This could help shape management decisions about which species to plant into the grassland areas, and what treatments are required to enhance their survival.

The effect of moisture and light levels that I found is only relevant for seedling growth during the dry season. In the wet season the treatments might not make such a difference, or may even be opposite as water stress is not an issue and light levels are lower. For example Gerhardt (1996) found high light levels inhibited growth in the dry season but increased seedling growth in the wet season. Duncan and

Chapman (2003) found seedling growth increased with the removal of non-tree vegetation, however this effect disappeared after two years. It would be beneficial to have this trial carried out over a longer period of time to see if similar effects are found. The second trial has been left set up to see if we can re-measure the seedlings in November 2014 to get seedling growth over a full year. This trial will be left to run for as long as we continue to get useable data.

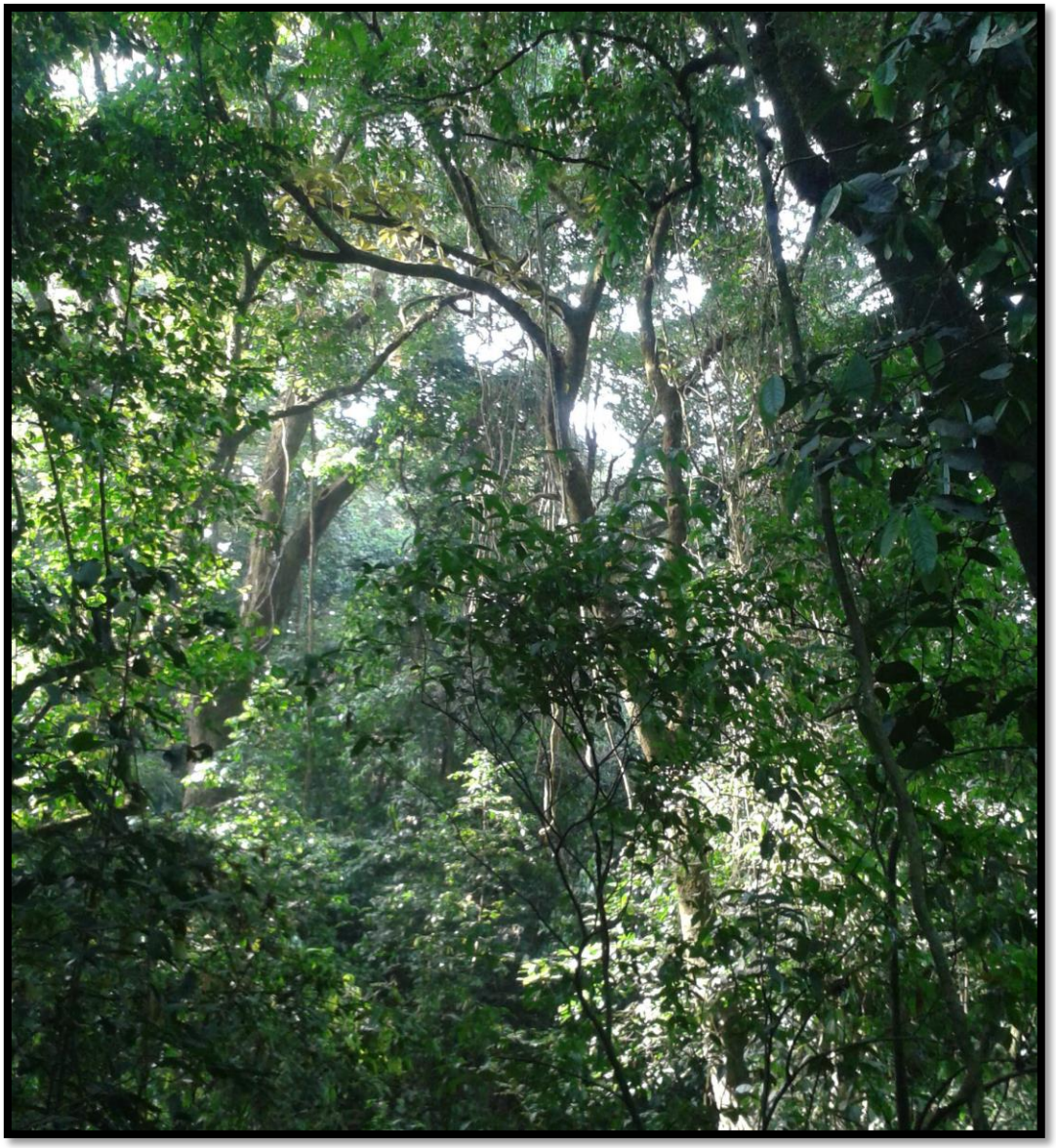
Attempting to calibrate the soil moisture data logger again will allow me to calibrate the data I have and so the soil moisture analyses can be re-done. The patterns found and significance of different effects will stay the same as it is a linear calibration. However the calibration would allow us to have the data in useable units.

4.5 Conclusions

The grass sward in this system does created a barrier restricting the growth and survival of seedlings establishing in the grassland. The success of the application of artificial shade was expected, but the reason for it was not entirely so. I expected lower light levels to be the main benefit of shade, but it appears to actually be the associated increase in soil moisture. The magnitude of this increase means that, if possible, shading newly planted seedlings will increase their chance of establishment. Although the removal of roots enhances the survival of seedlings statistically, it is a minor effect compared to that of shading. The relative impact of above-ground and below-ground manipulations appears to be system specific and possibly reflects the needs of the seedlings and the most limiting factors in that environment (e.g.. compare Holl (1998b) and Gerhardt (1996). If shading anyway, it may be decided that the cultivating is unnecessary and simply trimming grass may be adequate to create a positive effect. A possible advantage of cultivating that was not tested in this experiment may be that removing the grass totally creates a longer period of time for the seedlings to be free of the grass sward. A longer term study will be able to tell us if that is the case.

Chapter 5: Synthesis

Relevance to the Restoration Project, and Future Directions



5.1 Factors Restricting Natural Regeneration at Ngel Nyaki

Dispersal limitation

Seedling densities under the remnant trees I surveyed were much higher than in open degraded grassland. Based on the study I carried out it is difficult to distinguish the relative influence of higher dispersal under trees, and better growing conditions for the seeds that do arrive, on the observed pattern but both factors are likely to have an impact (Duncan & Chapman, 1999; Herrera & García, 2009). Barnes and Chapman (2013) found a significant drop-off in both the number and diversity of seeds in the seed rain with increasing distance into the grassland from the forest edge. I also found a relationship between the density of seedlings and the number of bird visitors to the above tree (Chapter 2). Since higher bird numbers equates to higher seed rain this implies that these seedlings are not at maximum densities under many trees and are limited by the amount of seed rain as opposed to environmental factors. As a large proportion of the birds observed in the grassland are small or forest edge birds there is the potential that tree species from the core forest, especially those with larger fruits, may be particularly dispersal limited in the grassland (Chapter 2).

Seed predation

Seed predation will have an effect on seedlings recruitment in any area where tree species are seed limited (Calviño-Cancela, 2007; Denham, 2008). As I found evidence for dispersal limitation (see above) seed predation will probably negatively impact forest regeneration into grassland areas at Ngel Nyaki forest. However while in many systems seed predation has been found to have a major effect on recruitment in grasslands (Bruun et al., 2010), particularly as there is often more predation in grassland areas relative to the core forest (Craig et al., 2011; Magrach et al., 2011), my results illustrate that at Ngel Nyaki this is not the case. In contrast, seed predation in the grassland at Ngel Nyaki is in fact lower than in the core forest, neither does it increase under isolated trees, which is most positive for restoration at Ngel Nyaki as it implies that seed predation is not a major factor restricting natural regeneration (Chapter 3).

Effect of the grass sward

Seedlings growing in the grassland appear to have their survival and growth restricted in the dry season by competition from the grass sward for limited water in the soil (Chapter 4). This is a significant barrier to natural regeneration as it restricts the establishment of naturally dispersed seedlings, and also the success of planting seedlings as a management option. The seedling species I used in my experiment did not seem to be affected by the high exposure to sunlight in the grassland compared to forest levels. The species I chose were both pioneer species so are better adapted to deal with high light levels than forest core species.

5.2 Recommendations for Restoration

Plant Tree Seedlings in Patches

Single trees or small clumps of trees in grassland are acknowledged as being important foci for restoration because they attract frugivorous birds which then disperse seeds below them (Uhl, 1987). Moreover, trees provide more suitable microsites for seedling growth under their canopies than in open grassland (Duncan & Chapman, 1999; Herrera & García, 2009). My study showed that this generalisation applies to the Ngel Nyaki system with more birds attracted to both individual and clumped trees, and higher seedling densities found under canopies than in the open (Chapter 2). However in contrast to several other studies (Holl & Lulow, 1997) seed predation rates under isolated trees were similar to that in open grassland (Chapter 3), despite the higher seed rain, allowing more of the seeds to escape predation and potentially germinate and grow.

Planting seedlings for restoration is a common practice and has been successful in many tropical systems (Parrotta & Knowles, 2001; Cusack & Montagnini, 2004). However, this can become very expensive so at Ngel Nyaki the size of the areas that are able to be restored through this method is

very restricted. In order to decrease the cost, while still ensuring that the process is effective in encouraging regeneration, my recommendation is to take advantage of the positive effects small patches of remnant trees have on natural regeneration, by trying to increase the number of tree clumps in the grassland areas. This approach to restoration has been suggested for other tropical systems (Nepstad et al., 1990; Hooper et al., 2005; Zahawi & Augspurger, 2006), and involves planting nursery-raised seedlings in many small patches throughout the fenced-off grassland areas. Planted forest does not need to be continuous as many birds are willing to travel long distances over regenerating grassland; I found no decrease in bird visitors to focal trees out to a distance of approximately 90m from the edge of the forest (Chapter 2). Planting five to 25 seedlings in small patches enables much larger areas of grassland to be actively managed with the same numbers of seedlings and planting resources, or similarly, the same area of land can be managed for much lower costs (Holl et al., 2011). Once these seedlings mature the patches of trees will attract birds and become foci of natural regeneration. Over time the patches will become bigger as new seedlings establish under the canopies, making the area even more attractive to birds. This snowballing effect will increase the speed of regeneration. Eventually these patches will merge into each other creating a closed canopy of secondary forest (Yarranton & Morrison, 1974).

The first comprehensive comparison of planting across whole areas ('plantations') as compared to planting in 'islands' (patches) (Holl et al., 2011) did show some negative effects of planting in patches. For instance, on average seedlings grew faster in plantations, possibly due to a smaller proportion of seedlings exposed to the harsher environmental conditions at the edge of planted areas. Similar survival rates of seedlings planted in islands as those planted in plantations, and a much lower overall cost, do help to negate this negative impact though. At Ngel Nyaki where financial restraints are high, I believe this still remains the best option for enhancing regeneration in the grassland areas.

Shading of planted seedlings

Due to the success of the artificial shade on the growth and survival of the seedlings I planted for this study (Chapter 4) I would recommend these small patches of seedlings to be planted in areas where

the grass has been trimmed at ground level, and some sort of shading has been provided for at least the first dry season after planting. Other studies have used portable shading devices made from shade cloth (Benayas et al., 2005), but as shelter made from wood and grass was sufficient in this study, and as these are cheap and biodegradable materials, there is no need to use shade cloth.

Choice of seedling species

Seedlings planted should be fast growing pioneer or forest edge species as they tend to be more tolerant and adaptable to the conditions found in the grassland (Bazzaz & Carlson, 1982). Species that are found naturally growing in the grassland already, including those seedlings found under trees in the seedlings survey (see Appendix 6.6), provide a list of potential species to begin planting with. Using fast growing species means less time before they are large enough to start attracting birds and to provide enough canopy cover for enhanced seedling growth. Species with fleshy fruits are recommended as they both attract frugivorous birds and also become a source of propagules in the grassland for further regeneration.

Under-planting forest core species

Once secondary growth is covering a large area it may be necessary to do another round of planting with some of the late-successional forest species (Griscom & Ashton, 2011). These species are often missing in regenerating forest for long periods of time due to dispersal limitation and/or microsite effects. Once the canopy cover is closed enough to create an environment conducive to the growth of these seedlings, this is a good way to ensure the species make-up of the original forest is mimicked in the secondary forest (Griscom & Ashton, 2011).

5.3 Suggestions for Future Studies

Ant secondary dispersal

Ant dispersal (myrmecochory) is the primary dispersal method of at least 3000 plant species from 80 families (Giladi, 2006). In some cases it seems that the removal of seeds to ant nests actually saved seeds from predation by rodents, as elaiosomes were removed and then seeds were discarded undamaged (Auld & Denham, 1999). There is also a growing realisation that many seeds that are primarily dispersed by vertebrates are secondarily dispersed by ants, leading to the issue discussed in Chapter 3 that removal rates from invertebrate only exclosures may not be an accurate representation of predation rates (Vander Wall et al., 2005). For instance in Costa Rica leaf-litter ants (*Pheidole* sp.) collect seeds from vertebrate faeces and remove them to their nests. Although most of these are consumed, approximately 6% are deposited intact onto refuse piles which are better microhabitats for the germination and growth of those seeds compared to the forest floor (Levey & Byrne, 1993). Documenting the fate of seeds removed by ants at Ngel Nyaki has the potential to add much to our understanding of seed dynamics, and the role of ants in dispersal of seeds in regenerating grassland.

In order to understand the role of ants as seed predators and dispersers at Ngel Nyaki I recommend:

- A comprehensive collection and identification of all the ant species present in the grassland at Ngel Nyaki and observations of how these ant species treat the seeds they collect. I began a preliminary study along these lines in January 2014 but due to time constraints more work is needed.
- Further seed removal experiments (similar to those I undertook), coupled with observations to follow the seed after it has been removed, including the distance moved and final seed fate (i.e. the proportion consumed vs proportion discarded intact). These types of experiments have been carried out in the Neotropics (Levey & Byrne, 1993; Renard et al., 2010), and Australia (Hughes & Westoby, 1992), although studies in Africa are rare. Due to the difficulties involved in tracking small seeds, many methods have been suggested to follow seed fate during and after ant dispersal. To measure dispersal distances of seeds that are

deposited on the ground surface, painting seeds with fluorescent paint then searching with UV light sources was suggested (Bossard, 1990). More recently Levey & Byrne (1993) used captive colonies of ants to which they fed known amounts of seeds to determine the proportions deposited intact onto refuse piles. Other studies have been undertaken by feeding painted seeds or known amounts of seeds to wild colonies then excavating the nest to retrieve unconsumed seeds (Hughes & Westoby, 1992; Renard et al., 2010). The appropriate method will depend on the ant species and site factors.

- Trials to test germination rates, seedling survival, and growth rates of those seeds deposited by ants into nests or refuse piles, as compared to seeds left on the surface. Again, there have been multiple solutions to the question of how to measure this. Levey & Bryne (1993) collected ant refuse piles and topsoil from the forest, and planted into them four-day old seedlings of the species they were studying. These seedlings were then grown in greenhouses to replicate light and moisture conditions. Hughes and Westoby (1992) fed a known number of seeds into a wild nest and measured the seedling emergence of that species from that nest, which was then compared to emergence rates of the same species from the forest floor.

Bat dispersal

Bats are important dispersers in many tropical systems, indeed in Mexico levels of bird and bat dispersed seeds in degraded grassland are similar (Galindo-González et al., 2000). Despite this there is a lack of studies about seed dispersal by bats compared to birds due to the added difficulties of monitoring nocturnal dispersers. Knowledge of bat dispersal is important as many seed species are exclusively dispersed by bats (Duncan & Chapman, 1999), bats have different habitat preferences and requirements from birds (Duncan & Chapman, 1999), and seasonal variation in the number of seeds dispersed varies differently between birds and bats (Galindo-González et al., 2000). Bats are present at Ngel Nyaki and are willing to cross areas of degraded grassland to reach roosting sites (pers. obs.) but the species present and their diet types are unknown. In order to determine the contribution of bats to seed dispersal at Ngel Nyaki I suggest the following studies:

- Mist-netting of bats to establish what species are present in the forest and their relative densities.
- Collect faecal samples from bats (Galindo-González et al., 2000), and carry out analysis of fruiting syndromes of trees in the forest to establish what species rely on bats for dispersal.
- An analysis of the seeds found in seed traps in the fenced grassland areas over the last five years, based on dispersal vector – bird or bat.
- A similar study set up to the one I carried out, but focusing on bats, would give a relative idea of bat use of the regenerating grasslands. This would probably involve the use of night vision cameras set up to view focal trees to record number and length of visits.
- Trials to determine the effect of artificial bat roosts in the degraded grassland. Through encouraging the use of these areas bat roosts have the potential to benefit natural regeneration by increasing seed rain and possibly seedling establishment (Reid et al., 2013). At least one of the species at Ngel Nyaki is willing to use artificial roost sites as demonstrated by the presence of many colonies in the roof spaces of houses.

Germination

If species are seed limited in grassland then direct seeding can be a low cost option for increasing diversity (Engel & Parrotta, 2001) instead of planting nursery grown seedlings. This strategy will enhance restoration if it is a lack of dispersal that is restricting the growth of these seedlings. However if there are other factors such as the microsite in the grassland not being suitable for the germination and survival of young seedlings then this will be a waste of time and money. In order to test if direct seeding is a viable option for introducing species into the regenerating system, a trial similar to Bonilla-Moheno and Holl (2010) or Cole et al. (2011) should be carried out.

- Choose a selection of tree species from which the seeds can be collected in large quantities, and are limited in the grassland. A range of both pioneer and forest species would be interesting to test for different responses.

- Direct seed these seeds into different habitats: open grassland, areas under tree patches, full secondary forest, and the core forest as a control.
- Measure germination rates, growth rates and survival rates of seedlings over a one or two year time period.

5.4 Conclusions

Limited dispersal, seed predation, and competition with the grass sward for water were all found to be factors that will restrict the natural regeneration of the degraded grassland around Ngel Nyaki forest. These and other barriers will cause regeneration to proceed very slowly, even within the fenced and protected areas. Despite this, the reduced seed predation in the grassland and evidence of the dispersal of some seeds and their subsequent germination below tree canopies does indicate that regeneration is occurring to some degree within these fenced off areas. Long-term vegetation surveys are necessary to track the progression of this regeneration over long time periods.

The recommended restoration plan is based on outcomes of this study and is designed to increase the speed and success of regeneration by taking advantage of the natural regeneration that is already occurring. The development of this plan, and any future plans, involves looking at the system from many different angles. Comprehensive plans will i) take advantage of the fact that some potential barriers to regeneration do not seem to be significant in this system i.e. seed predation in grassland and under remnant trees is low at Ngel Nyaki, ii) imitate the natural processes that have been shown to be effective in this system i.e. using remnant trees as foci for regeneration, and iii) manipulate specific environmental conditions that are preventing regeneration i.e. shading of seedlings. Further studies on the processes that are occurring in these areas will continue to develop a more well-rounded picture of the functioning of this forest-grassland system. Long term trials of seedlings planted in both plantations and 'islands' will contribute to the still sparse literature on these contrasting approaches to restoration plantings, while actively enhancing regeneration at these sites.

Appendix

Appendix 6.1 Tree characteristics for the 18 focal trees (Chapter 2).

Tree ID	Species	Site	Number of Bird Visitors	Average Stay Length	Height (m)	DBH (cm)	DFFE (m)	Canopy Area (m2)	Surrounding canopy cover (m2)	Canopy Density	Food Presence	Edible Fruit
1	*Psorospermum corymbiferum*	1	27	16	2	9.5	32	3.5	0	2	No	Yes
2	*Nuxia congesta*	1	67	40	7.5	33.5	32	7	1.5	4	Yes	No
3	*Trema orientalis*	1	27	44	3	7	27	7	3.5	3	No	Yes
4	*Nuxia congesta*	1	15	23	5.5	10	17	4	6	3	No	No
5	*Nuxia congesta*	1	12	17	3.5	11	32	8	1.5	3	No	No
6	*Syzygium guineense*	1	45	16	9	41.5	15	10	6	4	No	Yes
7	*Combretum molle*	2	134	53	7	9	35	2.5	75	2	No	No
8	*Maesa lanceloata*	2	92	84	2.5	20.5	30	4.5	2.5	2	No	Yes
9	*Syzygium guineense*	2	147	59	4	35.5	20	17	3	3	No	Yes
10	*Bridelia speciosa*	2	16	19	3.5	5.4	21	2	8	3	No	Yes
11	*Nuxia congesta*	2	170	64	9	20.5	75	15	9	2	Yes	No
12	*Bridelia speciosa*	2	136	43	7	41	90	40	15	4	No	Yes
13	*Bridelia speciosa*	3	113	70	6	28.5	17	20	6	4	No	Yes
14	*Combretum molle*	3	37	12	3.5	11.5	14	2.5	3	1	No	No
15	*Combretum molle*	3	227	36	8	40	35	30	12	3	Yes	No
16	*Bridelia speciosa*	3	57	36	5	24	50	15	18	4	Yes	Yes
17	*Albizia gumifera*	3	19	23	3.5	9	39	2	3	2	No	No
18	*Combretum molle*	3	23	9	5.5	15	17	1.5	26	1	No	No

Appendix 6.2 Photos of focal trees for allocating canopy density measures

Tree 2

Tree 3

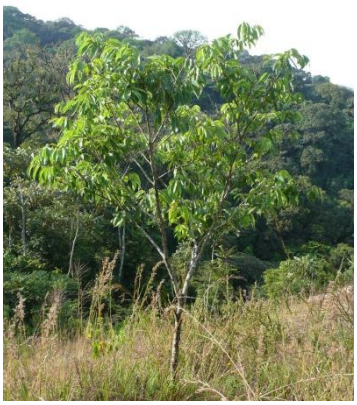
Tree 4

Tree 5

Tree 6

Tree 7

Tree 9



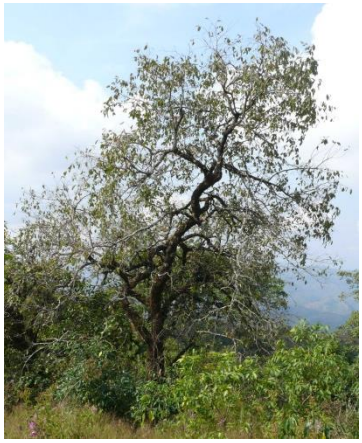
Tree 10

Tree 11

Tree 12

Tree 13

Tree 14



Tree 15

Tree 16

Tree 17

Tree 18

Photos for tree 1 and 8 have not been included due to missing photos.

Appendix 6.3 Extra information for the exclusion of tree 7 and isolation measurements when analysing the effect of tree characteristics on bird visitation numbers (Chapter 2).

When all trees were included in the analysis, the effect of isolation was significant. However this was suspected to be because of the large influence exerted by tree 7. As most of the trees had low levels of surrounding canopy, except for tree 7, this point created a significant trend (Fig. 6.3.1). The hat-value for the tree 7 point is 0.916 while the other 17 points have hat-values between 0.056 and 0.080. This shows that this point has a large amount of leverage on the model. When tree 7 was excluded from the analysis isolation became non-significant ($p = 0.359$) and canopy size and the presence of food were the two significant explanatory variables.

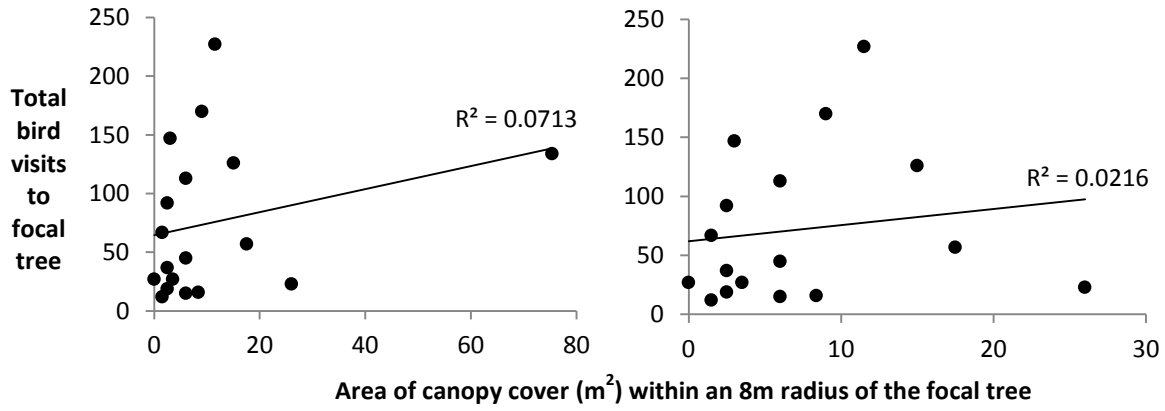


Figure 6.3.1 The relationship between the area of canopy cover in the 8m radius around the focal tree, and the number of birds that land on that tree, a) including all 18 trees, b) with tree 7 removed.

As I didn't survey any other trees with surrounding canopy areas of over $30m^2$ it is impossible to tell if the significant positive relationship between the area of surrounding canopy cover and bird visitations is a true biological pattern or if it is simply a relic of this data set. As a result I decided to exclude this point from this analysis and only look for a pattern in canopy areas under $30m^2$.

Appendix 6.4 List of all birds observed in grassland around the edge of Ngel Nyaki forest between November 2013 and February 2014 (Chapter 2).

Scientific Name	Species	Size (cm)	Diet	Preferred Habitat
Coracias abyssinicus	Abyssinian Roller	28-30	Insects or small vertebrates	Dry wooded habitats
Treron calvus	African Green Pigeon	25-28	Fruit	Forest, wooded savannah
Melocichla mentalis	African Moustached Warbler	19-20	Insects	Rank herbage in savannah
Ceyx pictus	African Pygmy Kingfisher	12	Insects, small fish and reptiles	Various habitats
Saxicola torquatus	African Stonechat	12.5	Insects, also seeds and fruit	Open habitats
Zosterops senegalensis	African Yellow White-eye	10-11	Mainly insects, also nectar, fruit, seeds	Wooded habitats
Ploceus bannermani	Bannerman's Weaver	14	Unknown; presumably seeds, insects and fruit	Montane forest and scrub
Hirundo rustica	Barn Swallow	15-19	Insects	Various habitats
Sylvia atricapilla	Blackcap	13.5-15	Insects and fruit	Dry scrub
Estrilda nonnula	Black-crowned Waxbill	11	Seeds, some insects	Grassland, forest regrowth
Apalis jacksoni	Black-throated Apalis	11.5	Insects	Forest
Merops variegatus	Blue-breasted Bee-eater	17	Flying insects	Various open habitats
Columba sjostedti	Cameroon Olive Pigeon	36-40	Fruit	Forest and wooded savannah
Emberiza tahapisi	Cinnamon-breasted Rock Bunting	14	Seeds and some insects	Open savanna with rocky outcrops
Pycnonotus barbatus	Common Bulbul	18-20	Fruit	Anything except closed forest
Chrysococcyx caprius	Didric Cuckoo	19	Mainly Insects, sometimes seeds	Various open and wooded habitats
Francolinus bicalcaratus	Double-spurred Francolin	30-35	Insects and plant matter	Grassland, farmbush, scrub
Lybius bidentatus	Double-toothed Barbet	23	Fruit and insects	Woodland
Euschistospiza dybowskii	Dybowski's Twinspot	12	Seeds and Insects	Wooded grassland
Sylvia borin	Garden Warbler	13-14.5	Berries and insects	Wooded and bushy habitats
Camaroptera brachyura	Grey-backed Camaroptera	12	Insects, occasionally fruit	Dense shrubbery
Halcyon leucocephala	Grey-headed Kingfisher	22	Mainly insects, also small vertebrates	Woodlands, forest clearings, farmland
Chrysococcyx klaas	Klaas's Cuckoo	18	Mainly insects, some fruit	Various wooded habitats
Andropadus virens	Little Greenbul	16.5	Fruit, also seeds and insects	Forest zone and forest-savanna matrix
Circus pygargus	Montagu's Harrier	40-50	Rodents, bids, insects	Open habitats
Melaenornis edolioides	Northern Black Flycatcher	20	Insects	Woodland
Sylvietta brachyura	Northern Crombec	9	Insects	Dry and wooded savannah
Cinnyris reichenowi	Northern Double-collared Sunbird	11.5	Nectar and insects	Open montane forest
Passer griseus	Northern Grey-Headed Sparrow	14	Mainly seeds, also flowers, berries, insects, fruit	Mainly towns and villages

Dryoscopus gambensis	Northern Puffback	15-17	Insects	Savanna woodland; forest clearings
Camaroptera chloronota	Olive-green Camaroptera	11	Insects	Lowland forest and savanna outliers
Cinnyris bouvieri	Orange-tufted Sunbird	12	Nectar and insects	Forest edge
Linurgus olivaceus	Oriole Finch	13	Seeds, buds and fruit	Montane forest
Melaenornis pallidus	Pale Flycatcher	15-17	Insects and some small fruits	Various types of woodland
Campephaga petiti	Petit's Cuckoo-shrike	20	Insects	Montane forest/forest patches
Ficedula hypoleuca	Pied Flycatcher	13	Insects, occasionally fruit or seeds	Various wooded habitats
Anthus leucophrys	Plain-backed Pipit	17	Insects and seeds	Various open habitats
Cisticola erythrops	Red-faced Cisticola	12-14	Insects	Various grassy and bushy habitats
Centropus senegalensis	Senegal Coucal	40	Large insects and small vertebrates	Open habitats with tall grasses
Nesocharis shelleyi	Shelley's Oliveback	8	Insects and seeds	Montane forest
Cisticola brachypterus	Short-winged Cisticola	10	Insects	Wooded grassland
Colius striatus	Speckled Mousebird	15-17	Fruit, flowers and leaves	Various open and wooded habitats
Cinnyris coccinigastrus	Splendid Sunbird	14	Insects and nectar	Wooded savanna
Galerida modesta	Sun Lark	14	Invertebrates and seeds	Various open grassy habitats
Prinia subflava	Tawny-flanked Prinia	11-12	Insects and other invertebrates	Various grassy and bushy habitats
Laniarius aethiopicus	Tropical Boubou	23	Insects, small vertebrates, occasionally fruit	Various wooded habitats
Cinnyris venustus	Variable Sunbird	10	Mainly nectar, also insects	Wooded savanna, clearings, farmbush
Ploceus nigerrimus	Vieillot's Black Weaver	17	Mainly insects, also seeds, fruit, berries	Forest clearings, forest edges
Ploceus cucullatus	Village Weaver	15	Insects, also seeds and fruit	Forest edge (montane)
Schistolais leucopogon	White-chinned Prinia	14	Insects and spiders	Forest edge
Phyllastrephus albigularis	White-throated Greenbul	17	Insects	Forest
Phylloscopus trochilus	Willow Warbler	11	Insects	Various wooded habitats
Cisticola galactotes	Winding Cisticola	12-15	Insects, some seeds	Moist habitats
Euplectes capensis	Yellow Bishop	11-14	Seeds and insects	Grasslands in montane areas
Hyliota flavigaster	Yellow-bellied Hyliota	13	Insects	Savanna woodland
Buphagus africanus	Yellow-billed Oxpecker	21-23	Ticks	Wooded savanna and bush
Serinus mozambicus	Yellow-fronted Canary	11-13	Seeds. Also flowers, fruit, nectar, insects	Open woodland
Pogoniulus bilineatus	Yellow-rumped Tinkerbird	10	Mainly fruit, some insects	Forest and woodland
Macronyx croceus	Yellow-throated Longclaw	20-22	Insects	Various grassy habitats

Appendix 6.5 Condensed data for seedling counts under the canopy of each focal tree (Chapter 2).

Tree ID	Number of Seedlings	Density of Seedlings	Number of Seedlings Species
1	29	8	3
2	62	9	6
3	21	3	3
4	18	5	7
5	19	2	8
6	51	5	6
7	31	12	6
8	38	55	6
9	68	4	8
10	9	5	7
11	386	26	4
12	98	2	12
13	22	1	10
14	13	5	8
15	181	6	4
16	52	3	11
17	4	2	8
18	8	5	3

Appendix 6.6 Characteristics for each seedling species found under focal trees (Chapter 2).

Species	Family	Number found	Successional State	Dispersal Method
Anthonotha noldeae	Fabaceae	2	Forest edge	Wind
Bridelia speciosa	Phyllanthaceae	208	Pioneer/savannah	Vertebrate
Clausena anisata	Rutaceae	53	Forest/forest edge	Vertebrate
Combretum molle	Combretaceae	6	Grassland/savannah	Wind
Diospyros monbuttensis	Ebenaceae	19	Forest	Vertebrate
Dombeya ledermannii	Sterculiaceae	2	Grassland/savannah	Ballistic
Entada abyssinica	Fabaceae	1	Grassland/savannah	Wind
Entandrophragma angolense	Meliaceae	1	Forest	Wind
Eugenia gilgii	Myrtaceae	139	Forest edge	Vertebrate
Leea guineensis	Leeaceae	34	Forest edge	Vertebrate
Maesa lanceolata	Myrsinaceae	3	Pioneer/savannah	Vertebrate
Newtonia buchananii	Fabaceae	2	Forest edge	Wind
Nuxia congesta	Stilbaceae	4	Forest edge	Ballistic
Polyscias fulva	Araliaceae	1	Forest	Vertebrate
Prunus africana	Rosaceae	1	Forest	Vertebrate
Psorospermum corymbiferum	Guttiferae	135	Grassland/savannah	Vertebrate
Psychotria peduncularis	Rubiaceae	122	Forest/forest edge	Vertebrate
Psychotria succulenta	Rubiaceae	698	Pioneer/forest edge	Vertebrate
Syzygium guineense	Myrtaceae	24	Forest/forest edge	Vertebrate
Zanthoxylum leprieurii	Rutaceae	5	Forest	Vertebrate

Appendix 6.7 Characteristics for the ten species of seed that were used in predation trials (Chapter 3).

Mean weight and mean dimensions are based on a random sample of 20 seeds. Hardness was allocated as soft = fingernail can mark, medium = shell of seed brittle but crushable with fingernail, hard = not able to be marked or damaged by fingernail.

Species	Family	Mean Weight	Mean Dimensions (mm)	Hardness	Colour	Dispersal vector
Celtis gomphophylla (Baker)	Cannabaceae	0.027g	4.0 x 4.0 x 4.3	2	Dark brown (dark)	Vertebrate
Croton macrostachyus (Hochst. ex Delile)	Euphorbiaceae	0.0185g	4.8 x 2.7 x 3.6	2	Dark brown (dark)	Ballistic
Combretum molle (R.Br. ex G.Don)	Combretaceae	0.022g (0.096)	9.3 x 2.7 x 2.7) (17.4 x 10.6 x 4.4)	1	Green (medium light)	Wind
Entandrophragma angolense ((Welw.) C.DC)	Meliaceae	0.558g (0.6475 with wings)	3.7 x 20.4 x 24.4 (5.1 x 25.7 x 106.1)	1	Light brown (medium light)	Wind
Leea guineensis (G. Don)	Leeaceae	0.044g	5.1 x 4.2 x 3.7	3	Red (medium dark)	Vertebrate
Newtonia buchananii ((Baker) Gilbert & Boutique)	Fabaceae	0.119g	52 x 6.5 x 0.7 (55 x 9 x 1)	1	Red	Wind
Pittosporum viridiflorum (Sims.)	Pittosporaceae	0.020g	1.8 x 0.9 x 1.5	2	Red	Vertebrate
Polyscias fulva ((Hiern) Harms.)	Araliaceae	0.0016g	1.2 x 1.5 x 4.1	3	Cream (light)	Vertebrate
Psycotria peduncularis ((Salisb.) Steyerm)	Rubiaceae	0.036g	4.8 x 1.9 x 3.4	3	Cream (light)	Vertebrate
Sterculia tragacantha (Lindl.)	Sterculiaceae	0.523g	14.5 x 10.0 x 10.0	2	Dark blue (medium dark)	Ballistic

Appendix 6.8 Photos of 10 seed species used for seed predation trials.

Psycotria peduncularis

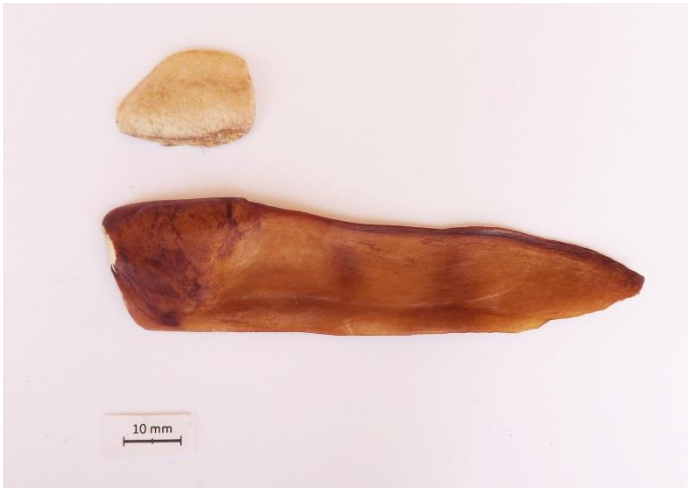
Combretum molle

Croton macrostachyus

Polyscias fulva

Leea guineensis

Celtis gomphophylla



Entandrophragma angolense

Sterculia tragacantha

Appendix 6.9 Seed treatment observations from seed predation study

Approximately ten *S. tragacantha* seeds were recovered from piles with what appeared to be ant grazing marks on them (Fig. 2.17). It appeared it was just the soft coat that was removed and the seed seemed still intact, therefore for the analyses these seeds were counted as not predated. Samples of both grazed seeds and intact seeds have been planted in the Ngel Nyaki nursery to check this assumption.

Some of the smaller seeds (*C. macrostachyus*, *C. gomphophylla* and *P. fulva*) were sometimes found with their endosperms removed and the shell left behind (Fig. 2.18). Seeds like this were only found in the grassland habitats of both Sites 1 and 3. In most other cases the seed was removed completely – assumedly either the entire seed was consumed, or it was transported away before the outer shell was discarded. Occasionally ants would be observed in the seed stations and interacting with the seeds. Those ants found in the grassland habitats tended to be much smaller than those in the forest habitats. Further study to see if these observations are indeed linked would be interesting especially since a similar pattern was found in Australia where they identified two guilds of ants based on their body size and treatment of the seeds. As very little is known about the specific ant species at Ngel Nyaki some samples have been collected and sent for identification.

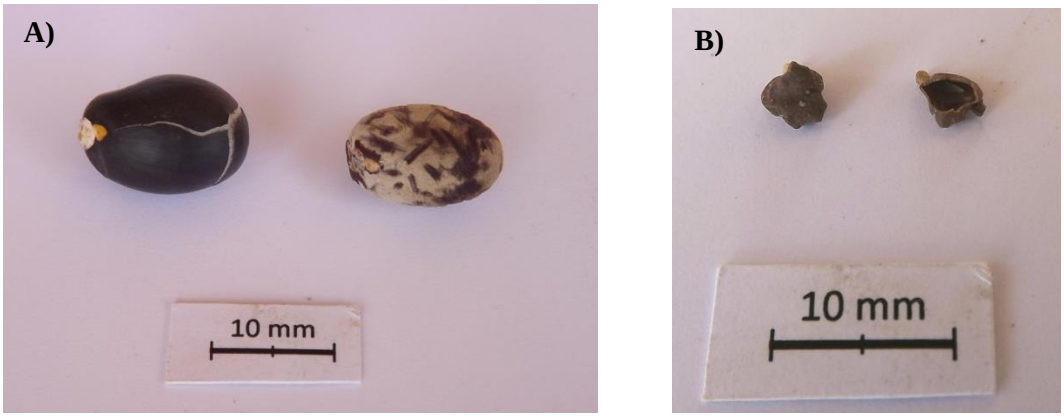


Figure 6.8 A) Two *S. tragacantha* seeds one has its coat still attached (left) coat still attached, the other shows sign of ant grazing (right). The viable seed is assumed to start at the be the brown/red layer and appears to be undamaged. B) Intact *C. macrostachyus* (left) and one with just the shell left (right).

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